THE MORPHOLOGY OF SOME CRITICAL BRAZILIAN SPECIES OF CYPERACEAE[1]

LIENE TEIXEIRA EITEN[2]

ABSTRACT

Eight taxa comprising six Brazilian species of Cyperaceae originally described in six different genera are redescribed in detail from the type collections and amply illustrated. Incorrect data and interpretations by the original authors are corrected.

Syntrinema brasiliense Radlk. & Pfeiffer is accepted as an independent genus and species. The original description of the inflorescence units was based on material which is not of this genus. The genus has pseudanthia, but these are of a type not found in the Mapanieae (the only tribe of Cyperaceae up to now known to have undoubted pseudanthia). The genus is placed in the newly described tribe, Syntrinemeae. Besides bisexual pseudanthia, the pseudospikelets also contain male pseudanthia lacking pistils and possibly neutral ones also. Instead of laminar glumellas as in the Mapanieae, the glumellas are bristles.

Chamaegyne pygmaea Süss. is shown to be a new species of *Eleocharis* series *Tenuissimae*, *E. chamaegyne* L. T. Eiten. The basal laminas that form the tiny tufts are not vegetative leaves but glumes and associated scales of the basal spikelets.

Helonema estrellense Süss. is shown to be an aquatic phase of *Eleocharis minima* Kunth. Topotype material collected and cultivated submersed in an aquarium retained the flaccid, filamentous *Helonema* vegetative form and remained sterile. When cultivated in moist soil and allowed to grow in the air, ramets of the same topotype clone formed small tufts of typical *Eleocharis minima* with abundant ripe achenes.

Bisboeckelera paporiensis Süss. is shown to be *Diplacrum longifolium* because the glume-like scales which enclose the pistils are free as in *Diplacrum*; the pistil is not enclosed in a utricle as in *Bisboeckelera*.

Micropapyrus viviparoides Süss. is accepted as an independent genus and species, and is put into the newly described tribe, Micropapyreae, because its pseudanthia are different from both the Mapanieae and from *Syntrinema*. Its glumellas are bristles.

The New World *Websteria submersa* (C. Wright) Britton is considered to be conspecific with the Old World *Scirpus confervoides* Poiret under the combination *Websteria confervoides* (Poiret) Hooper, and the varieties *W. submersa* var. *negrensis* Süss. and *W. submersa* var. *luetzelburgii* Süss. are not recognized.

Among the many existing problems in the family Cyperaceae, that of the branching patterns of the ultimate units of the inflorescence are particularly important since the correct subdivision of the family must be largely based on this character. Of the six species chosen for exposition in this article, three are known only from the type collection in one herbarium. Another species, although widespread and common in its terrestrial form, also occurs as a very different looking aquatic form which has been rarely collected and has been described as a new genus. The only descriptions of these four taxa are the original ones, which are confused and full of errors, making it impossible to recognize the true structure of the inflorescence. The fifth species is rare in herbaria; the sixth is

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[1] I wish to thank Dr. George Eiten for translating this paper to English and for providing the Latin descriptions; Dr. J. Murça Pires for the loan of Cyperaceae from the Instituto Agronômico do Norte, Belém, Pará; and the director of the Staatsherbarium München for the loan of types. Dra. Rosa Vilani Drummond kindly cared for the clones of the topotypes of *Helonema* which were planted at the agricultural station at Km 47, Rio de Janeiro State. During 1974, this work was supported by a grant from the Conselho Nacional de Pesquisas.

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ANN. MISSOURI BOT. GARD. 63: 113–199. 1976.

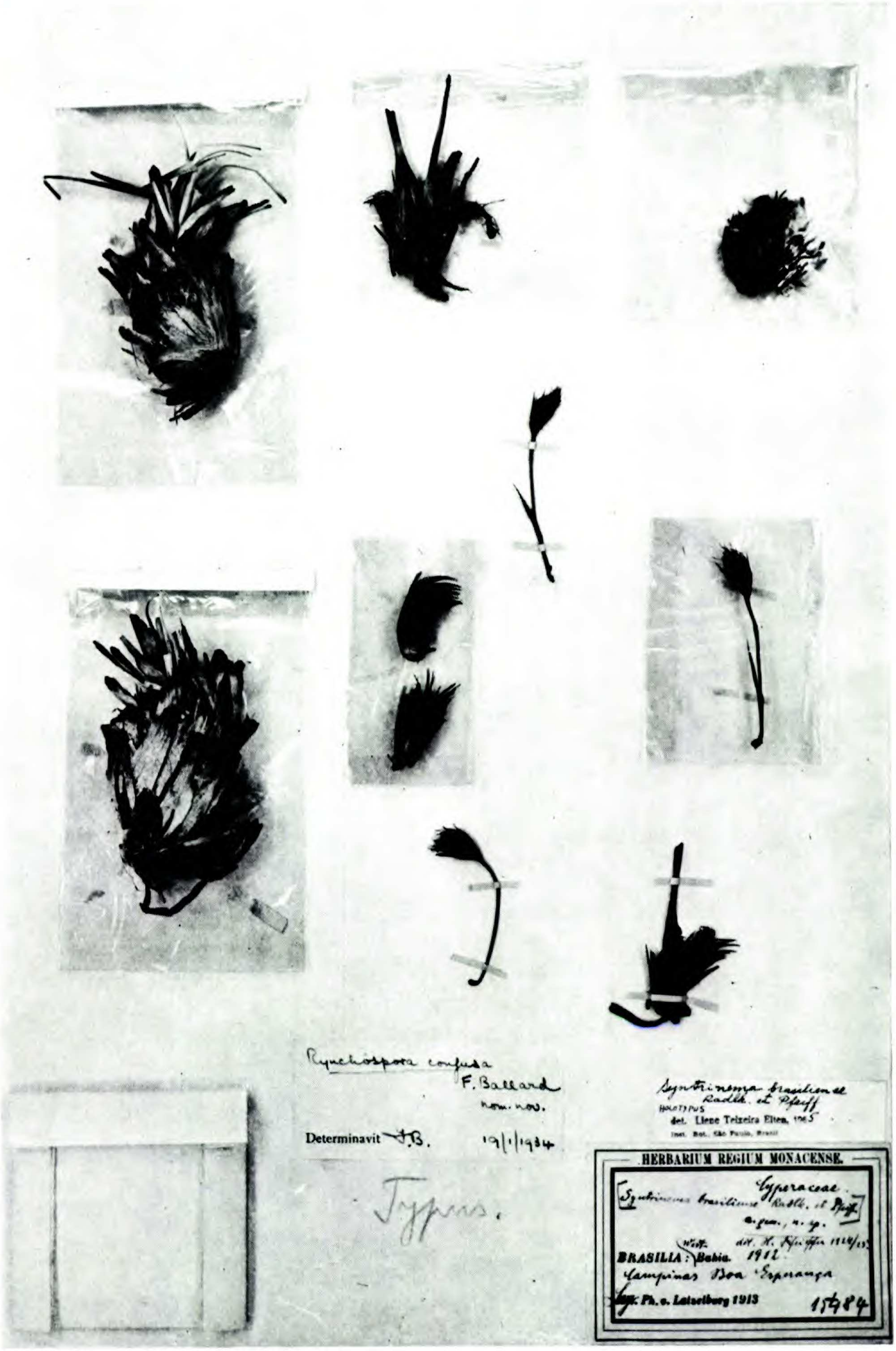


FIGURE 1. Lectotype of *Syntrinema brasiliense* Radlk. & Pfeiffer, *Luetzelburg 15484*; × 0.4. (For "Holotypus" on annotation label, read "Lectotypus.") The following drawings of this species, Figs. 4–20, were made from plants of this sheet.

FIGURES 2–3. Syntypes of *Syntrinema brasiliense* Radlk. & Pfeiffer; × 0.2—2. *Luetzelburg 1223.*—3. *Luetzelburg 15843.*

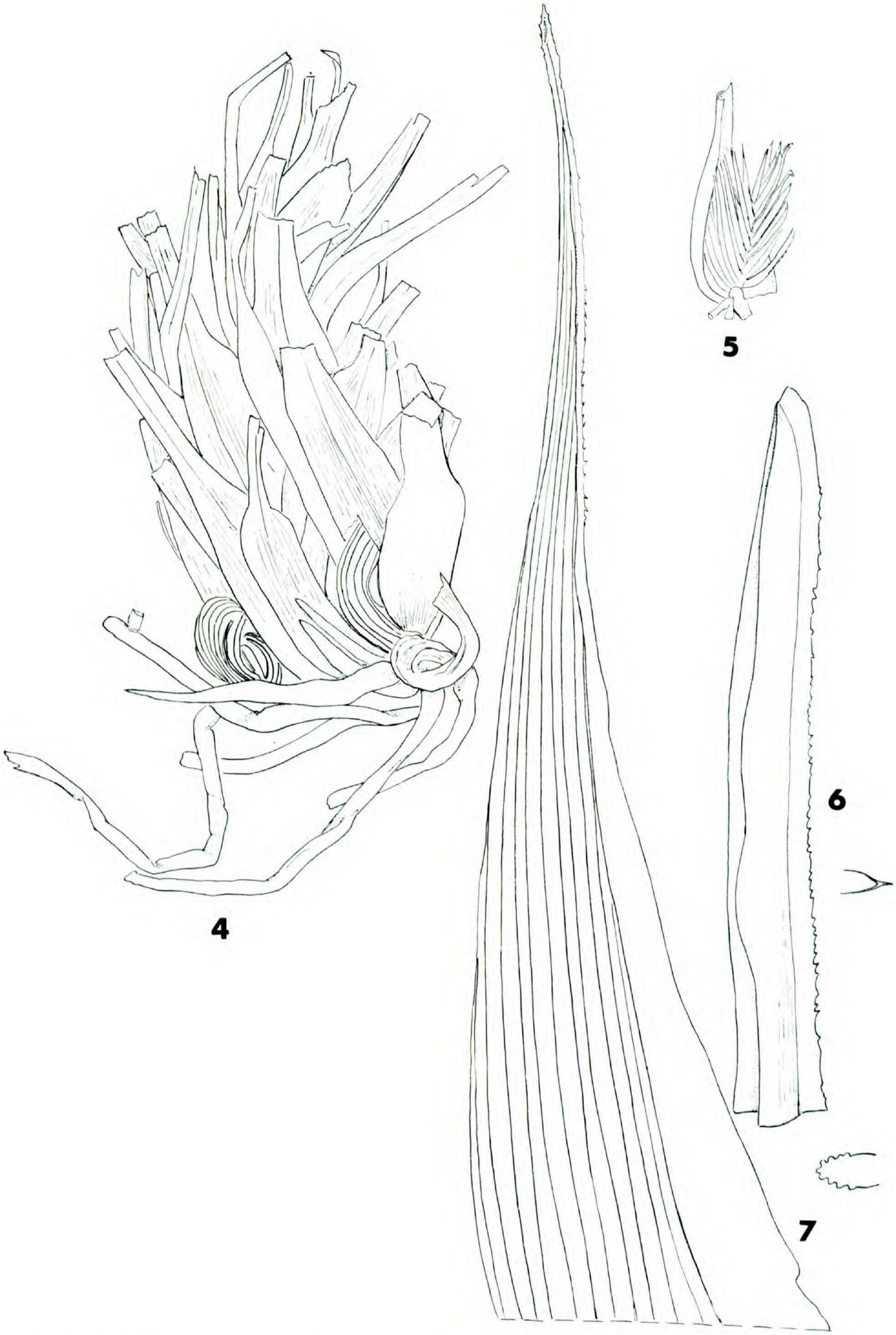
a common species but the variety of branching patterns in its inflorescence has never been described before.

The selected taxa illustrate the range of problems which a cyperologist may encounter in his study of the morphology of the family. An extreme ecological situation may radically change the habit of the plant, the number of glumes and flowers in the spikelet, and affect the sex of the flowers (*Helonema estrellense* Süss.). Plants which have suffered these modifications cannot be correctly identified based only on herbarium material; it is necessary to cultivate the plant in different conditions to produce structures which are more typical of the species.

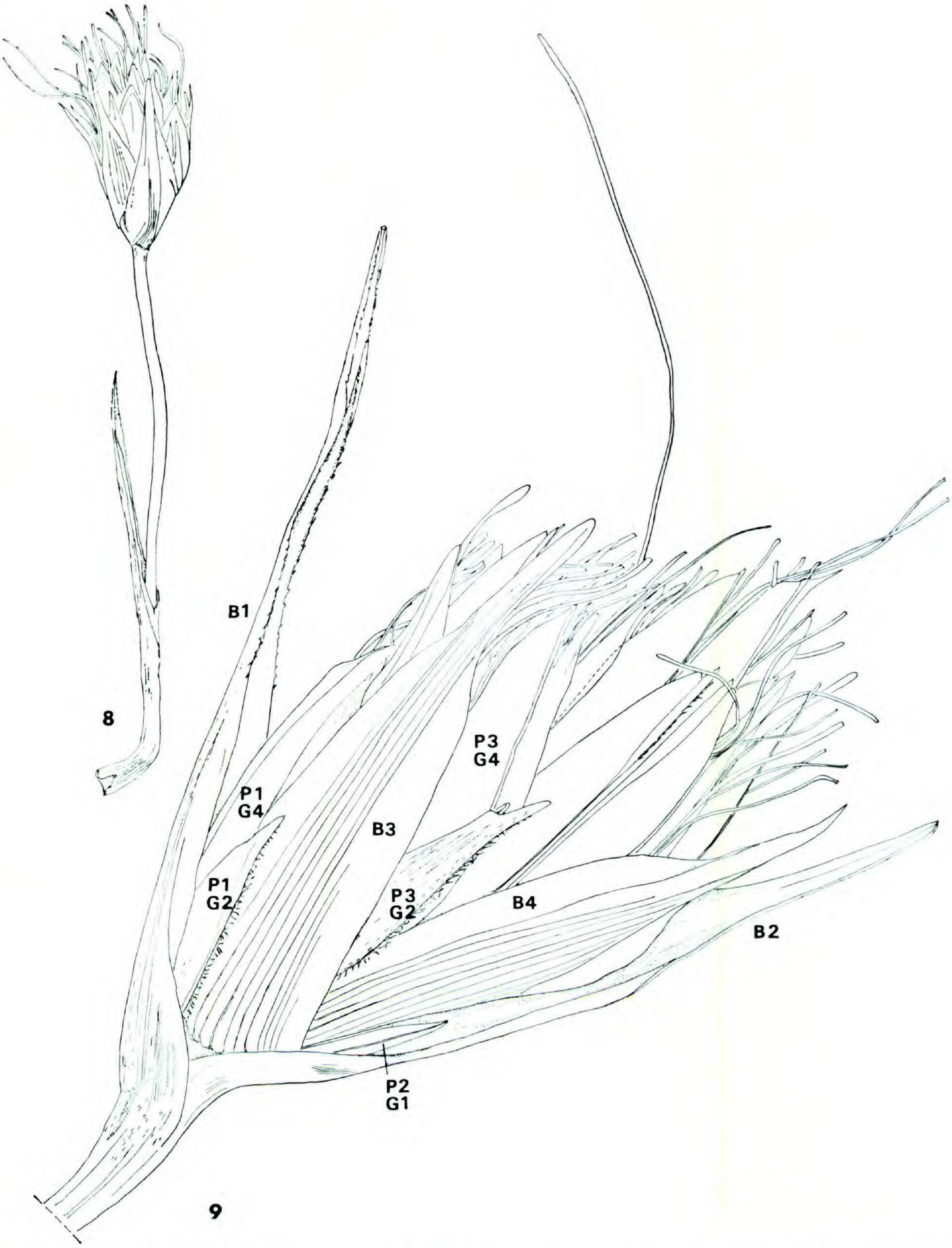
Variability in the composition of the spikelet in the same individual (*Helonema estrellense*) or in the branching pattern of the ultimate inflorescence units (*Bisboeckelera paporiensis* Süss.) requires that many parts of an inflorescence be analyzed.

Types of inflorescence branching patterns which are new for the family may be found (*Syntrinema brasiliense* Radlk. & Pfeiffer, *Micropapyrus viviparoides* Süss.), a possibility still open for material from little collected regions. Discoveries of this type may necessitate changes or additions in the higher units of subdivision of the family.

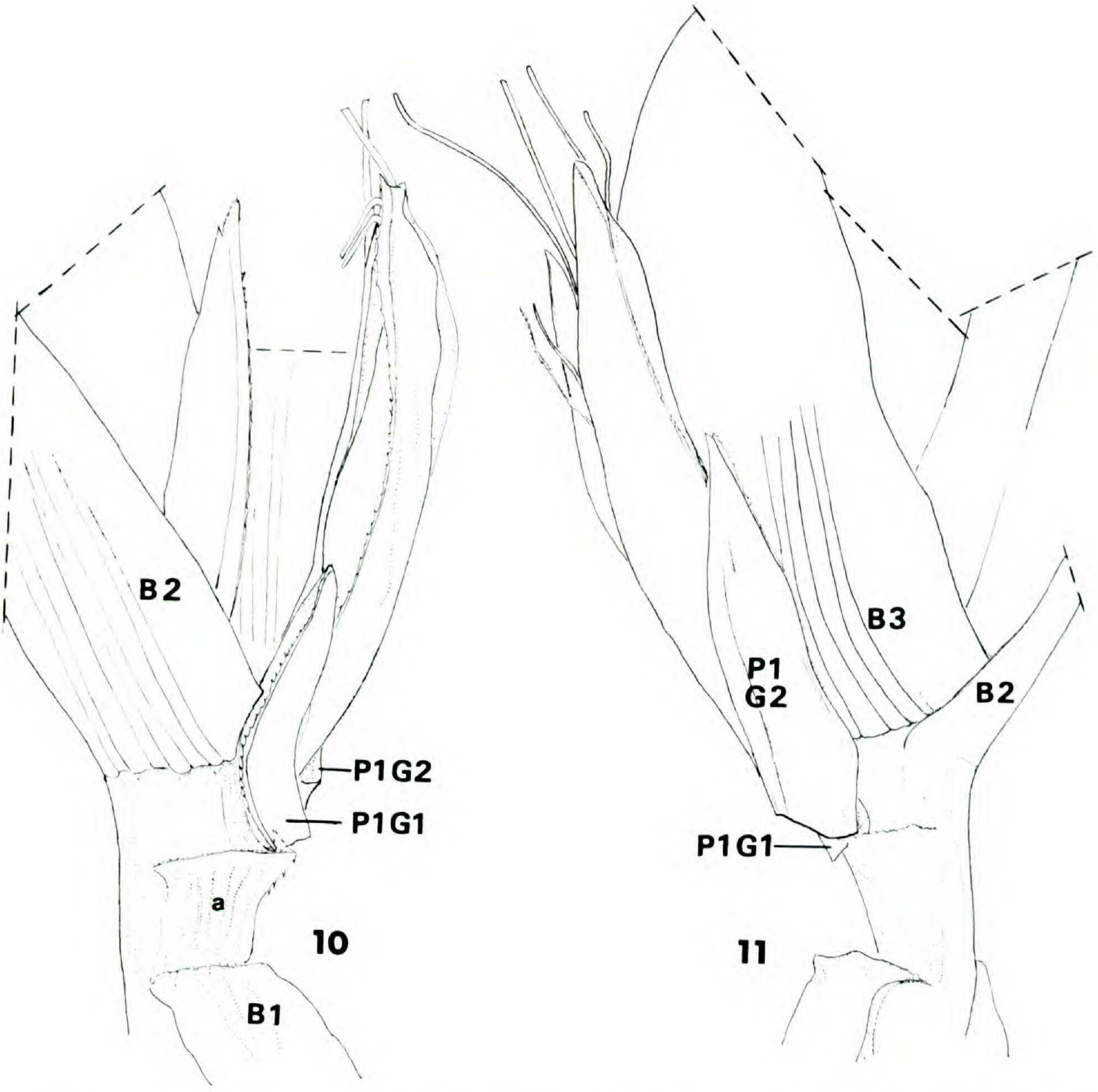
The validity of infraspecific taxa, such as varieties of *Websteria confervoides*



Figures 4–7.—4. Base of clump showing thick roots, two small shoots, and leaf bases; × 1.1.—5. Adaxial view of a small shoot and the base of its subtending leaf; × 1.1.—6. Upper part of a basal leaf of a small shoot showing naviculate form (open to left), with rounded apex and winged, denticulate keel at right; × 16. To the right is a cross section.—7. Upper part of an apical leaf of a small shoot showing canaliculate dorsal surface, membranous margin, and acuminate apex; × 16. To the right is a cross section.



FIGURES 8–9.—8. Peduncle (culm) with tubular prophyll and capitate inflorescence; × 1.4.—9. Capitulum; × 10.4. B1 = bract subtending first (lowest) pseudospikelet. B2–B4 = bracts subtending the second, third and fourth pseudospikelets, respectively. P1G2 = second glumiform bract of the first pseudospikelet; P1G4 = fourth glumiform bract of the first pseudospikelet; P2G1 = first glumiform bract (prophyll) of second pseudospikelet; P3G2 and P3G4 = second and fourth glumiform bracts of the third pseudospikelet. Note elongated filaments (from which the anthers have fallen) exerted from the tips of the pseudospikelets.

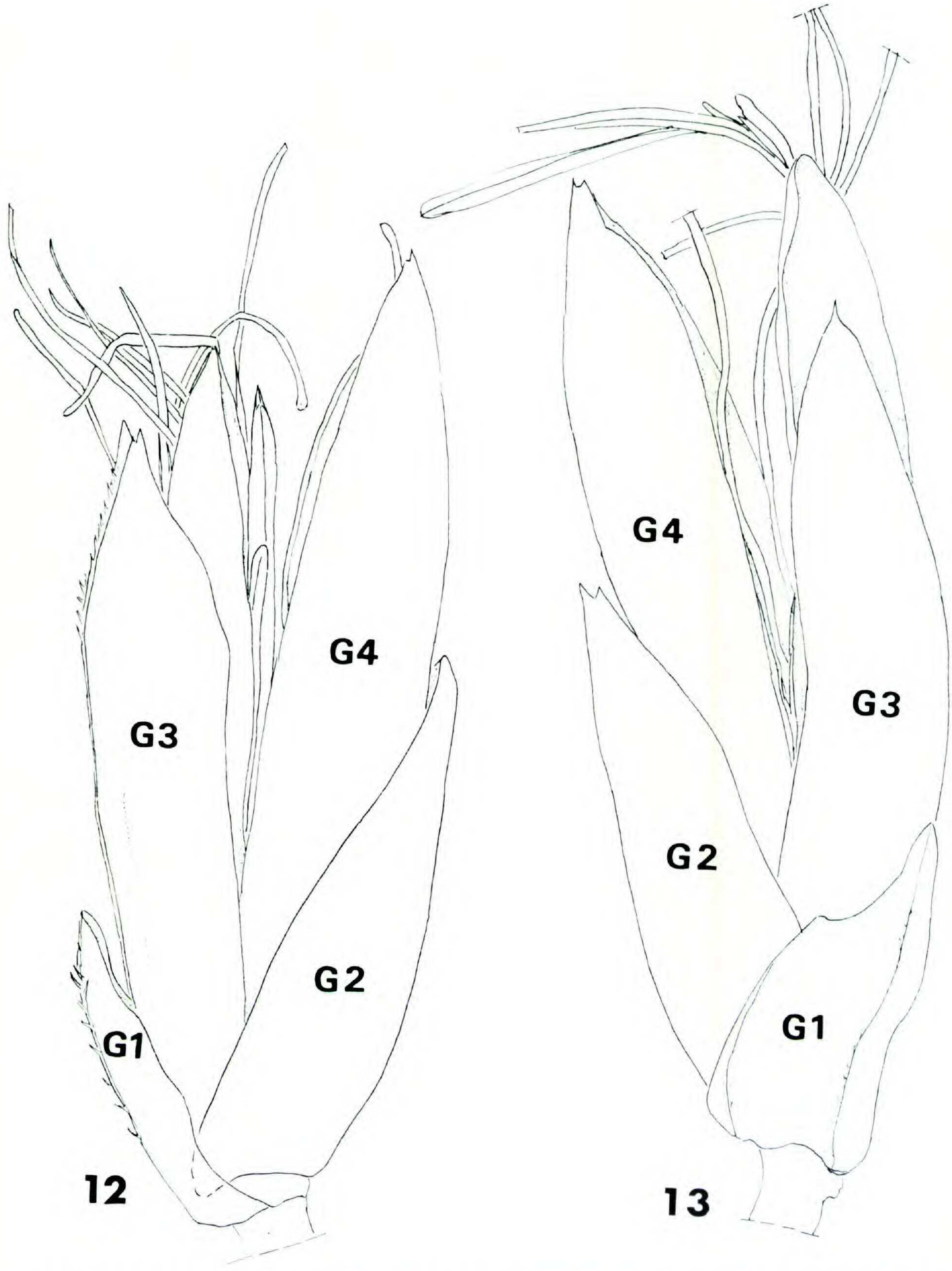


Figures 10–11. Base of capitulum shown in Fig. 9; × 15.—10. Bract B1 has been lowered and partially torn from its axis, leaving the scar, a. This bract subtends the lowest pseudospikelet in the head, shown on the right side. The level of emergence of bract B2 is further up the axis of the capitulum than that of B1.—11. Other side of the same capitulum, showing the level of emergence of bract B2 above that of B1.

(Poiret) Hooper (including *W. submersa* (C. Wright) Britton), can only be resolved by studying a sufficient number of collections from over the range of the species to see whether gaps in the variation pattern are sufficiently great.

There are cases where a collection represents a distinct species which shows a certain relationship to a known genus without falling into it perfectly. It then becomes necessary to decide whether to widen the morphological limits of the genus to include this species or to establish a new genus for it (*Chamaegyne pygmaea* Süss.).

As a result of this morphological study, I present new descriptions of type collections in which structures have been badly described in the original publica-



FIGURES 12–13. Abaxial and adaxial views of pseudospikelet P1 showing glumiform bracts G1 (prophyll), G2, G3, and G4; × 20. The prophyll and G2 are empty. Note prophyll G1 with its two characteristic veins and retuse apex.

tions. When it has been necessary to correct the identification of the material examined, the correct name of the species is given in parentheses below the name of the type, at the beginning of each description.

The *Chamaegyne*, *Helonema*, *Bisboeckelera* and *Websteria* collections were

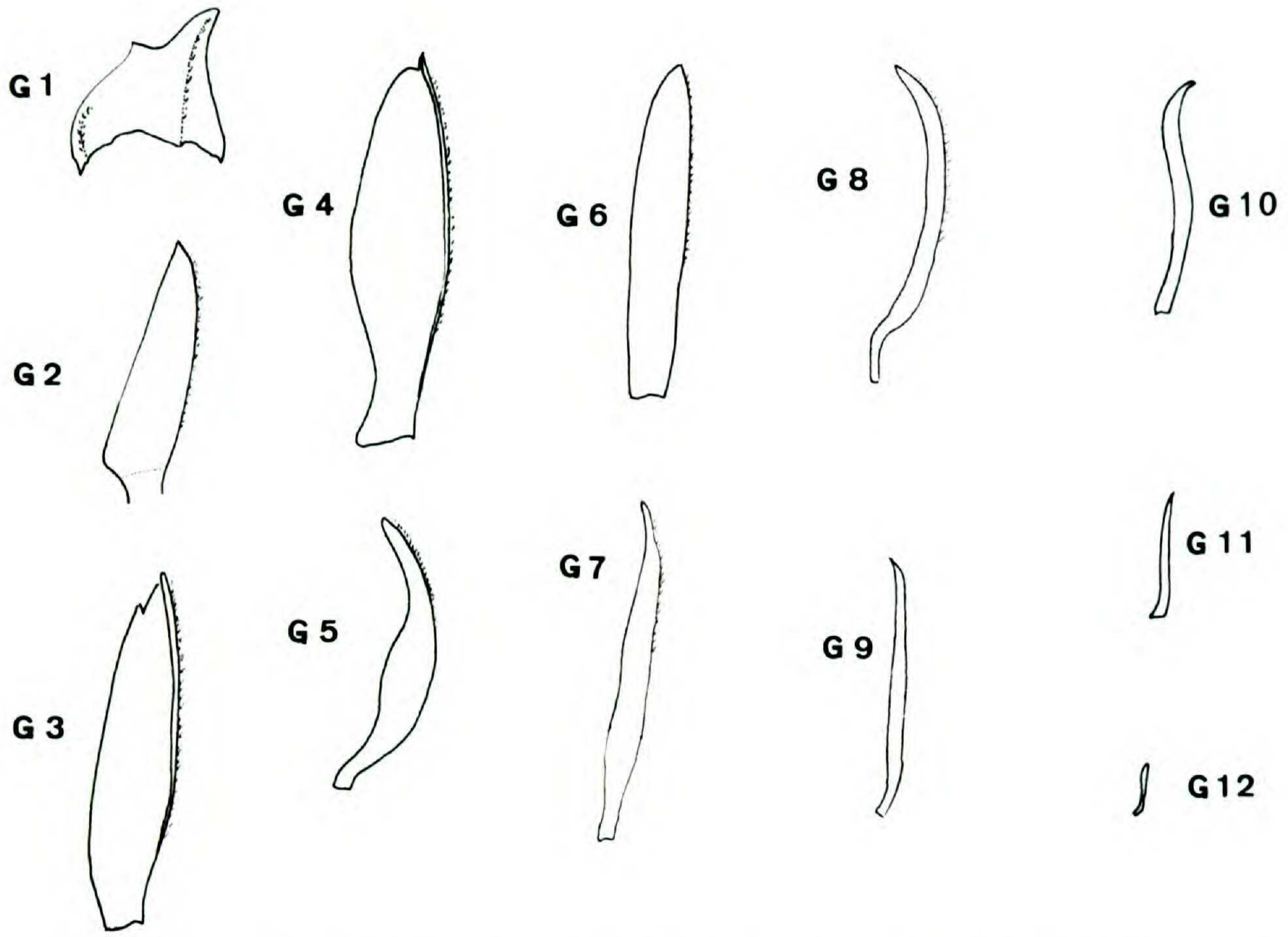


FIGURE 14. Glumiform bracts of pseudospikelet P1 arranged in order from base to apex; × 4.4. G1 is the prophyll, shown in abaxial view. G2 to G12 are in lateral view, opening to the left and with the midvein to the right.

treated in a brief preliminary fashion without illustration in Eiten (1970, 1972). Along with *Syntrinema* and *Micropapyrus* they are here treated much more fully.

In the descriptions and discussions which follow, a basic distinction is made between "terminal" and "lateral" flowers. Clearly, every flower is terminal in relation to the stem whose tip is its floral axis. Therefore, a lateral flower is lateral in relation to another stem from which the floral axis stem arises, which in the case of true spikelets is the rachilla. In the one-flowered spikelets of certain species of *Cyperus* (sensu lato), *Eleocharis*, and other genera, most of whose species have many-flowered spikelets, the flower seems terminal on the rachilla although, by comparison with related species, it is obviously really lateral, that is, pseudoterminal. The case is not so clear in the Mapanieae and the Bisboeckelereae, for in these tribes there is an apparently terminal pistil (female flower) on an axis, while lower down on the same axis laterally arise single stamens (male flowers) in the Mapanieae or spikelets of male flowers in the Bisboeckelereae. The Lagenocarpeae are claimed to have a spikeletlike structure with a terminal female flower also; however, evidence has been given in the previous article (Eiten, 1976) indicating that the apparently terminal pistil is actually lateral. I believe that all flowers in the Cyperaceae are basically lateral but this will have to be proved individually for each genus or group of related genera either by direct evidence or by a convincing analogy.

SYNTRINEMA BRASILIENSE Radlk. & Pfeiffer

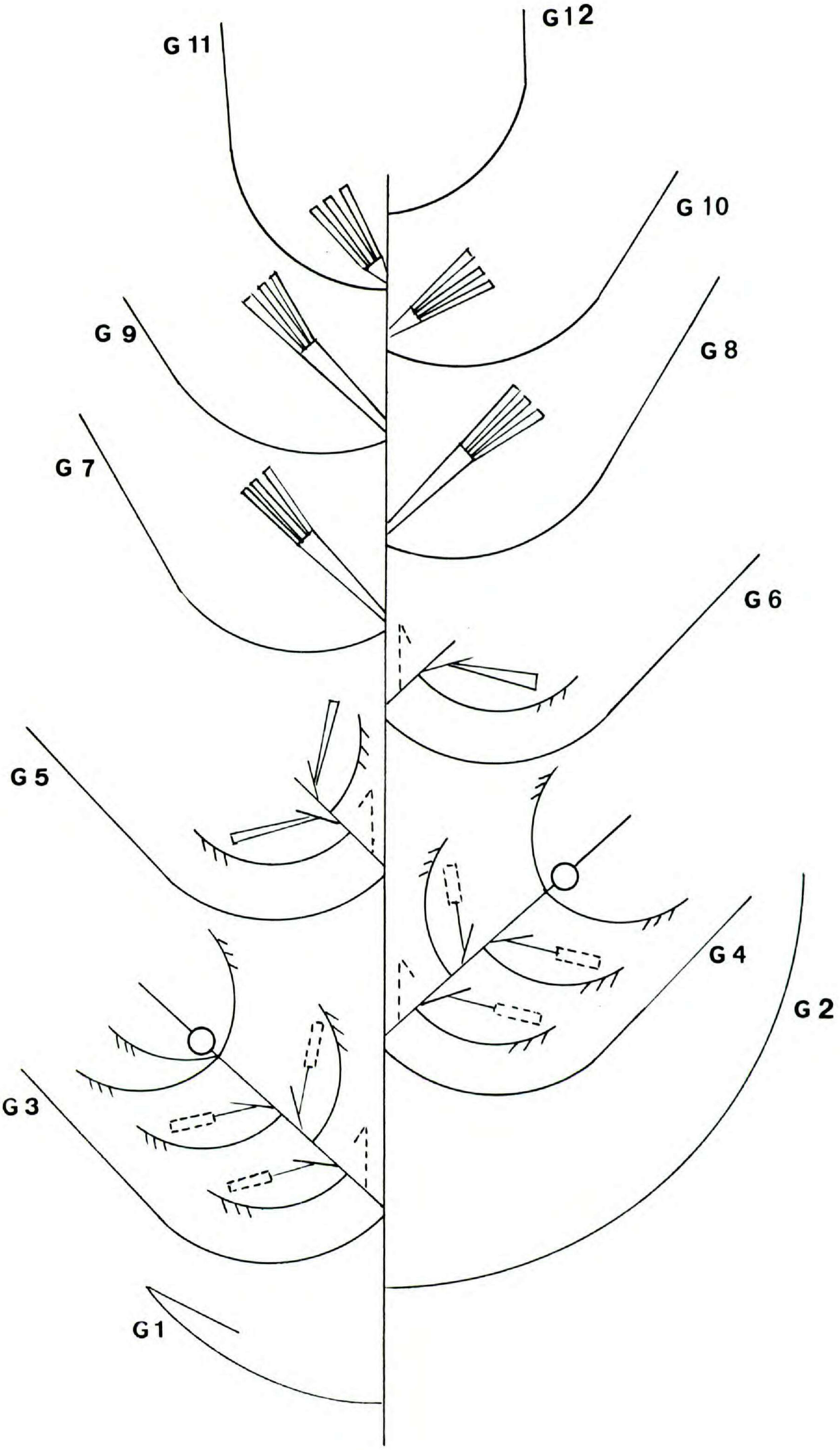
Description of the lectotype of *Syntrinema brasiliense* Radlk. & Pfeiffer, Repert. Spec. Nov. Regni Veg. 21: 238–239. 1925: Brasilia, West Bahia, Campinas Boa Esperança, 1912, *Luetzelburg 15484* (M). Photographs of the other syntypes seen: Brasilia, Goyas, Aug. 1912 *Luetzelburg 15843, 1223* (both M).

The plant forms clumps 10–20 cm tall. The leaves are imbricate and widened at the base. In the collection examined, the apices of the leaves had been destroyed by fire (Figs. 1–4). Straight or curved, small vegetative shoots occur in some leaf axils (Fig. 5); these shoots have two types of leaves, both longitudinally folded and distichously arranged (Figs. 6–7). Each culm bears a tubular prophyll at its base and a capitulum at its apex (Fig. 8). The capitulum is composed of approximately 9 or 10 pseudospikelets arranged spirally on an axis which is the continuation of the culm (Figs. 9–11). A bract subtends each pseudospikelet; the two basal bracts are longer, equalling or exceeding the capitulum (Fig. 9, B1–B2). On the axis of the pseudospikelet there are 11–12 glumiform bracts distichously arranged (Figs. 12–13, G1–G4; 14–15). The two basal bracts and the most distal bract are empty; the others subtend pseudanthia, i.e., very reduced ultimate inflorescence units which look like flowers (Fig. 15). The two lower pseudanthia are bisexual (Figs. 15–16, 21); an apparently terminal pistil is surrounded by 2–3 hypogynous bristles which appear to arise at the same level (Figs. 17–19). Below these bristles there are three more bristles arising at different levels on the rachilla, each subtending a male flower of a single stamen (Fig. 17). A gynophore can be made out attached to the young pistils (Fig. 18) but it is not so visible in the more developed pistils. The style is long and undivided.

The upper pseudanthia lack pistils. The lower two of these have bristles subtending what appear to be the filaments of male monandric flowers (Fig. 15, in the axils of glumiform bracts G5 and G6). In the lower of these two pseudanthia there are two bristles which appear to arise at the same level; in the upper of the two there is only one bristle or none. These bristles are more delicate than those in the bisexual pseudanthia. More material in other stages of flower growth would have to be examined to see if the filaments in these two pseudanthia really bear anthers (which therefore had fallen off in the material seen) and in which case the pseudanthia are male, or whether they are only staminodes in which case the pseudanthia are neutral.

In the more distal pseudanthia there are what appear to be functional male flowers. The pseudanthium consists of a column which is 3-lobed in cross section and which is shorter in the more distal pseudanthia. The column bears three large anthers at its apex (Fig. 20). The column consists of the three filaments fused together; the rachilla and bristles are perhaps also fused with them. Since the stamens in the lower bisexual pseudanthia are clearly each separate flowers, it is highly probable that the three stamens in the upper male pseudanthia are also each a separate male flower although they are fused together by their filaments. A unisexual pseudanthium has not been reported before in the angiosperms so far as I know.

Further details are given in the legends to the figures.


G 11
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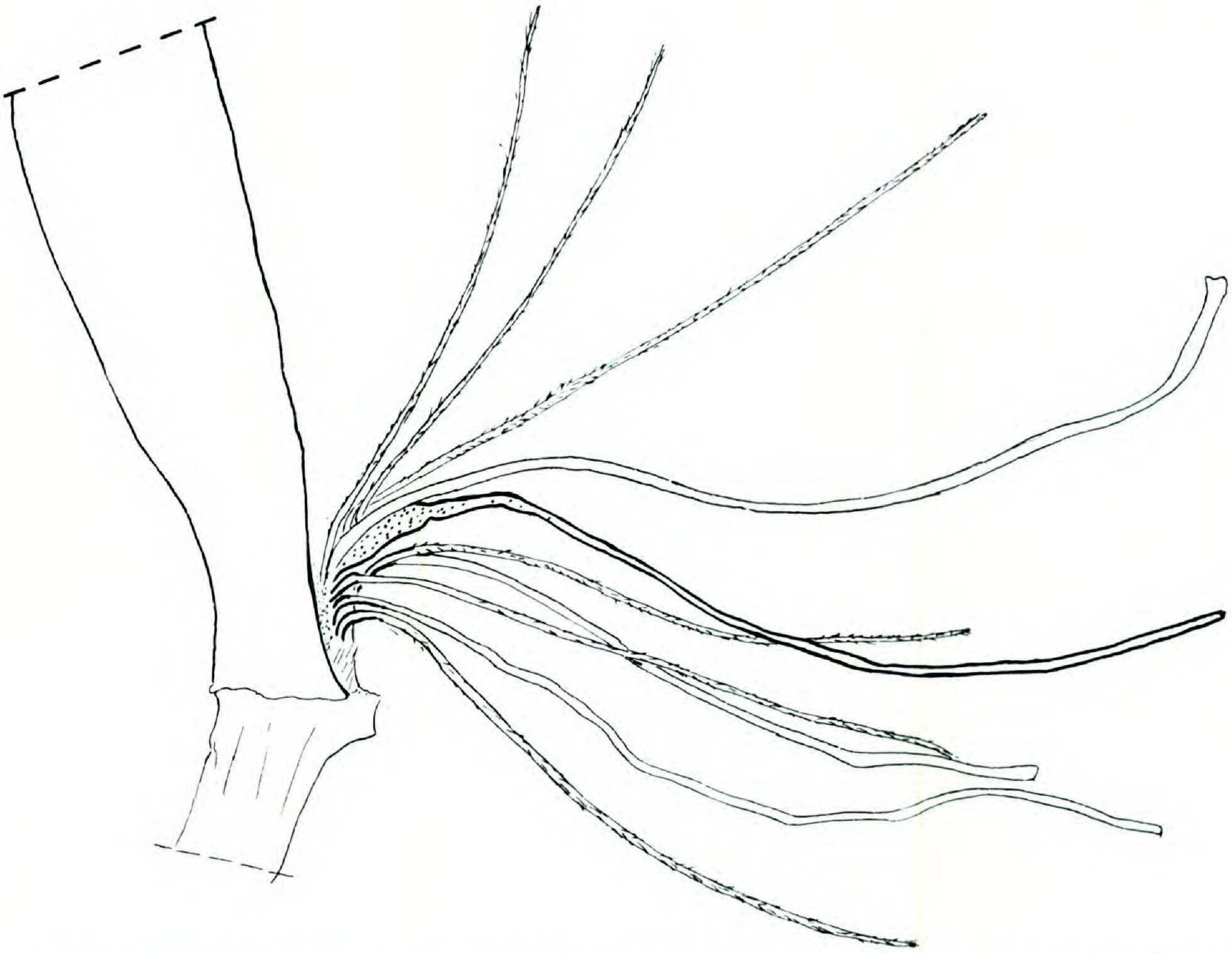

FIGURE 16. Base of pseudospikelet P1; × 25. The basal glumiform bracts, G1, G2 and G3, have been removed showing the lowest pseudanthium, PA1, appearing like a flower. Note 6 pilose bristles, 3 glabrous filaments from which the anthers have fallen, and a young pistil with a narrow ovary and long undivided style.

The genus *Syntrinema* has only one species, *S. brasiliense*, known only from its three syntype collections. The original description of the genus and species contains several errors. After having studied the syntype material, I found that the original description was based on a mixture of plants of different genera. The illus-

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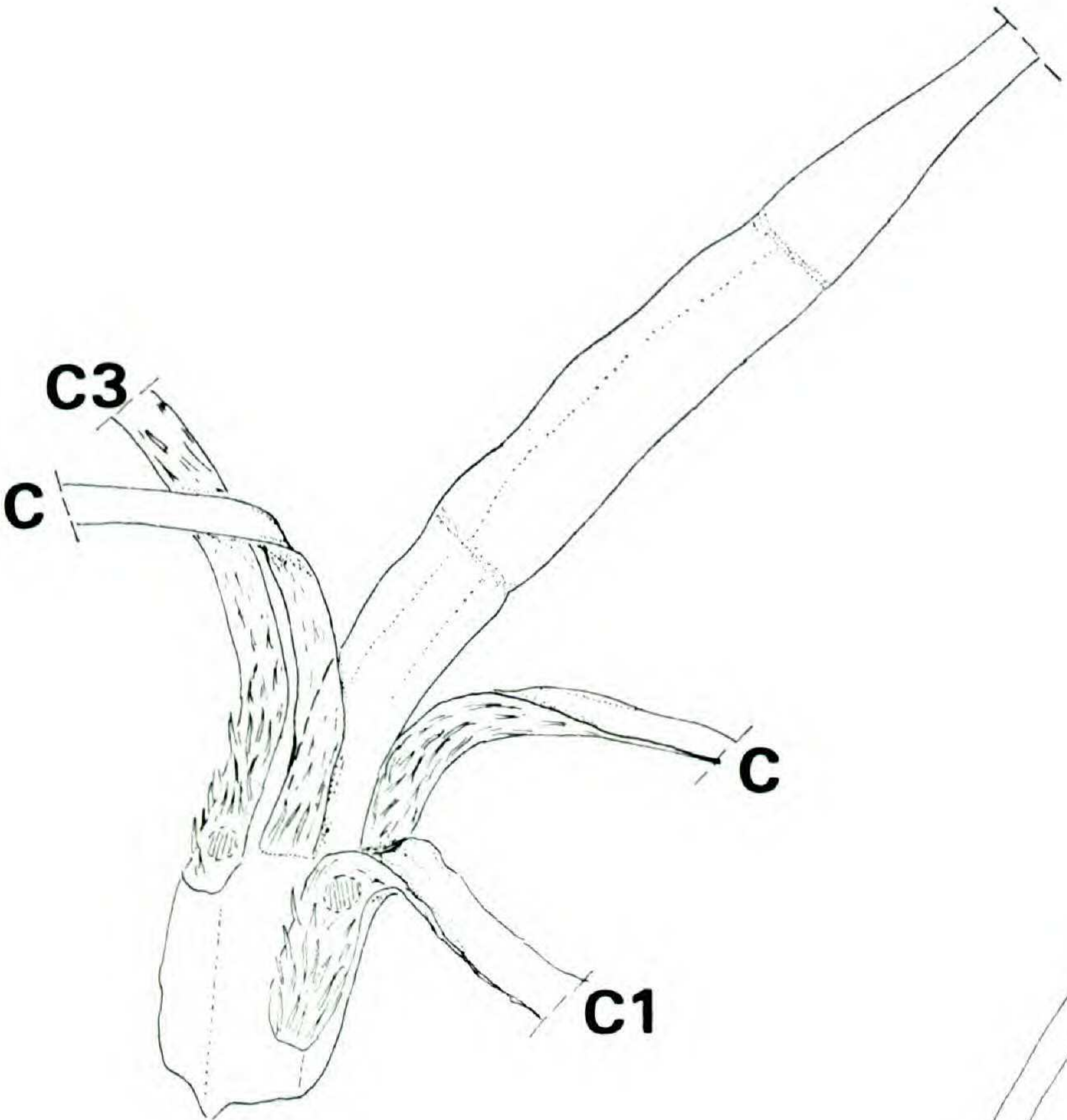
FIGURE 15. Branching pattern of basal pseudospikelet P1. The glumiform bracts, G1 (prophyll) and G2 are empty. Bract G3 subtends the pseudanthium PA1 (illustrated in Figs. 16–19), which has three basal bristles arising at different levels, each subtending a male flower of one stamen from which the anthers had supposedly fallen when the plant was examined, and three bristles at the base of the pistil. The bract G4 subtends the pseudanthium PA2, similar to PA1 but with two hypogynous bristles. Bract G5 subtends an apparently male pseudanthium PA3, which has two bristles and two structures which appear to be thick filaments or fused filaments. Whether these had anthers which fell off or whether anthers never developed is not known for certain. Bract G6 subtends a similar, apparently male pseudanthium PA4, which consists of one bristle and one filament structure similar to that in PA3. Bracts G7, G8, G9 and G10 subtend male pseudanthia, each consisting of a column (3-lobed in cross section) formed by the fusion of three filaments with the rachilla; there may be bristles fused here also. Three free anthers occur at the apex of the column. Bract G11 subtends a similar male pseudanthium but much less developed, with three anthers difficult to distinguish. Bract G12 is reduced and empty and covers over the tip of the pseudospikelet rachis. The pseudospikelet is essentially distichous but sometimes it is difficult to trace the two files of glumiform bracts. The hooked broken lines indicate the position that the prophylls of the pseudanthia would have if they existed.



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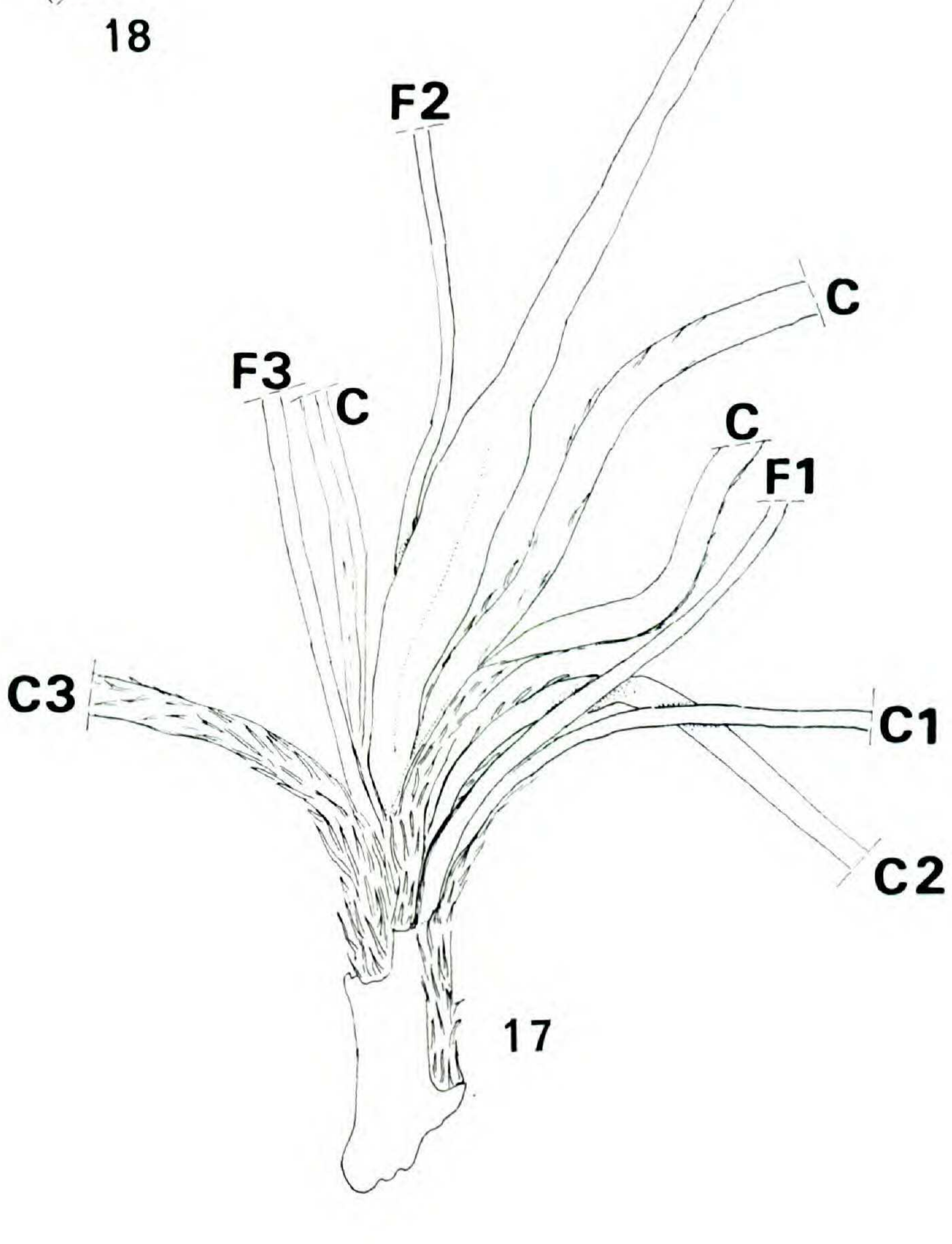

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tration of the habit given in the original publication corresponds to the species treated here. But the description and illustrations of the inflorescence unit are not that of *Syntrinema*. Pfeiffer (1925) gave a floral diagram of a pseudanthium with a terminal pistil surrounded by four empty glumellas and then by eight stamens, each in the axil of a glumella. The arrangement of stamens and glumellas is in a spiral except for the two outermost glumellas which are lateral. The glumellas are illustrated in other drawings in lateral and dorsal views. No bristles are shown. When Pfeiffer described the genus, he clearly stated that *Syntrinema* does not possess bristles ("Setae squamulaeque nullae"). The pistil seen by Pfeiffer has "Ovarium 2-loculare (an semper?)" and the style is distinctly bifid. An ovary with two locules never occurs in Cyperaceae. I suppose that there was a lapse or an error of observation here or the author examined material of another family for this character.

The difference between the characters described by Pfeiffer and those which I found in the type are considerable. The reason for the divergence is that Pfeiffer used material of another genus when he described the inflorescence unit of *Syntrinema*. I found in an envelope glued to the lower left corner of the herbarium sheet of *Luetzelburg 15484* (see Fig. 1) fragments of inflorescence units that were not of *Syntrinema* but which correspond to the drawings and description of the units given by Pfeiffer. The illustrations are of the unit of *Chorizandra*, a genus which does not occur in Brazil. This can be seen by comparing the Pfeiffer drawings with the figures of Tab. CXIX of Clarke (1909). Pfeiffer's Figs. c, d, e and g are respectively equal to Clarke's Figs. 4, 5, 3 (*Chorizandra sphaerocephala* R. Br.) and 11 (*C. enodis* Nees). Pfeiffer's floral diagram (his Fig. b) for *S. brasiliense* corresponds to the floral diagram of *C. sphaerocephala* (Fig. 7 of Clarke) in number and arrangement of parts except for one more stamen in the *Syntrinema* diagram.

In the same article in which Pfeiffer describes *Syntrinema brasiliense*, he included a key to genera of the Mapanieae, to which *Chorizandra* belongs. It is possible that in preparing this key he studied specimens of *Chorizandra* and by mistake returned the examined fragments to the envelope of *Syntrinema*. That his drawings are so similar to those of Clarke that they seem like tracings is even more peculiar.

Syntrinema has been placed under *Rhynchospora*. Ballard (1934) thought that the three syntypes of *S. brasiliense* were a new species of *Rhynchospora*; in

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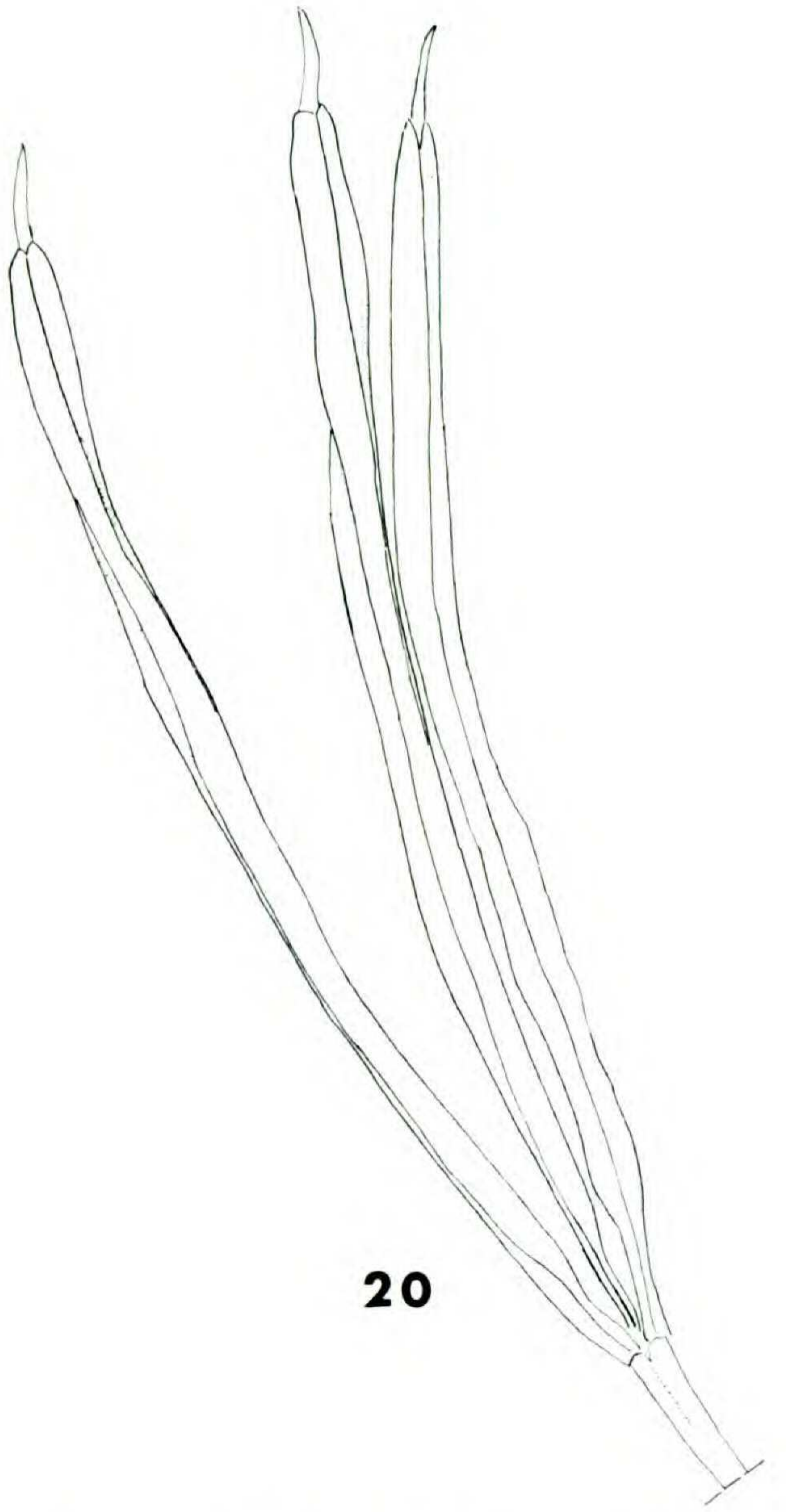
FIGURES 17–19. Details of pseudanthium PA1, showing insertion of bristles and filaments; × 56.—17. Bristles C1, C2, and C3 arise at different levels and subtend filaments F1, F2, and F3. The three upper bristles, C, apparently arise at the same level around the base of the pistil. The filaments are glabrous; the bases of the bristles are pilose on the abaxial side.—18. The two small shaded circles at the base of bristles C3 and C1 indicate the scars left when filaments F3 and F1 were pulled off. The scars are on the axis and in the drawing are seen through the bristle bases. The insertion at the base of the ovary of the bristle C whose base is visible is above that of the insertion of filament F3 which is not shown in this drawing. The base of all the bristles is laminar but the upper part, shown in Fig. 19, is terete. In the pistil in Fig. 18, two transverse lines delimit the young ovary; the axis below the lower line, which supports the ovary, is a gynophore.



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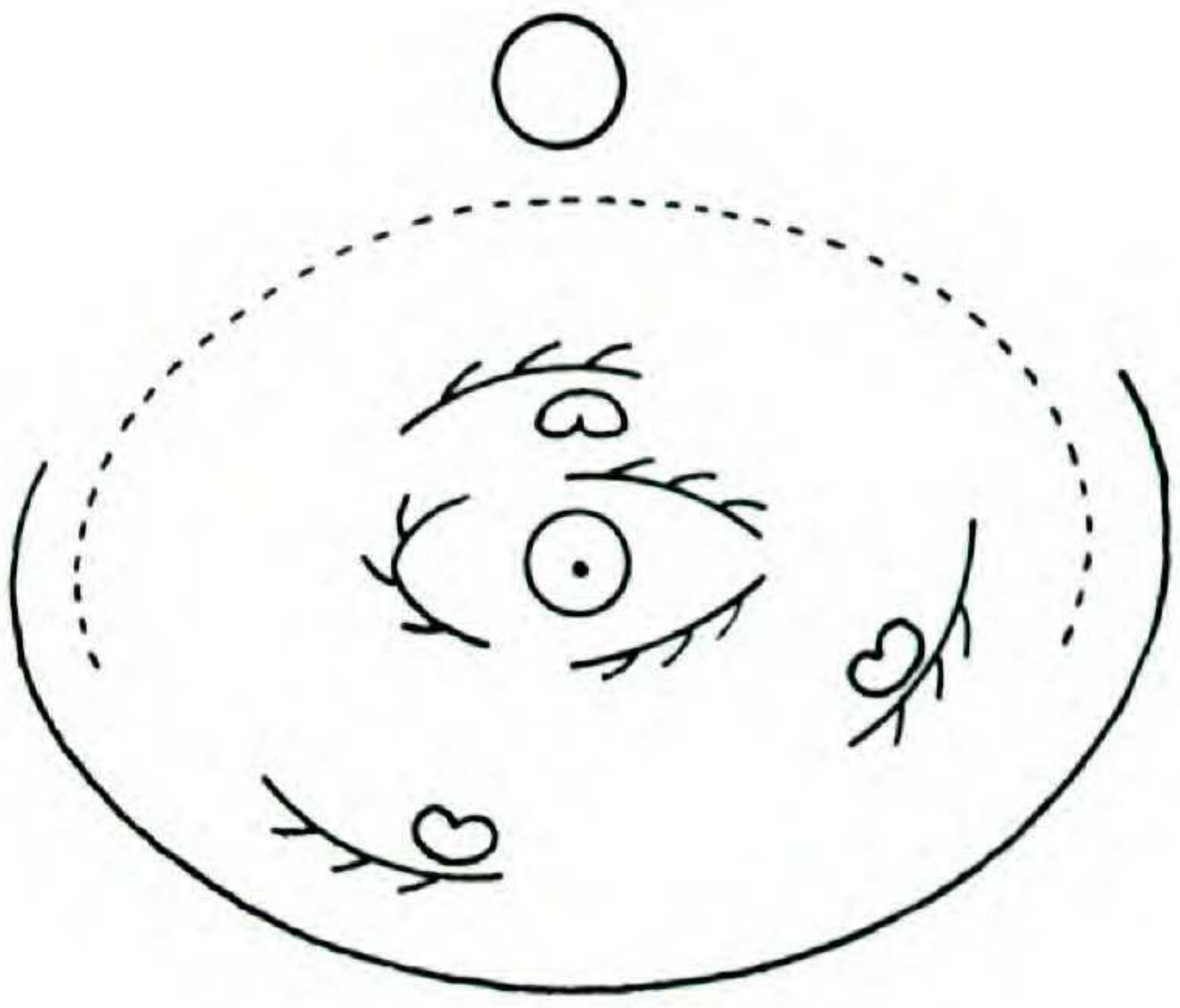

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FIGURES 20–21.—20. Three stamens with filaments united into a column; × 25. This constitutes the male pseudanthium PA5.—21. Floral diagram of pseudanthium PA1. Compare with branching pattern in Fig. 15. The upper circle represents the axis of the pseudospikelet; the solid curve is the glumiform bract which subtends the pseudanthium; the broken-line curve represents the position the prophyll would have if it existed. The six hachured lines are bristles, three subtending the male flowers of one stamen and three around the pistil.

1934 he annotated the sheets "*R. confusa* F. Ballard" and published the name. Hutchinson (1959) included *Syntrinema* in the synonymy of *Rhynchospora*. Koyama (1967) recognized *Syntrinema* as a separate genus and placed it in his subtribe Mapaniinae of the tribe Mapanieae. Because of the floral diagram given by Pfeiffer (but which really is of *Chorizandra*) Koyama thought that *Syntrinema* was similar to the genera of the subtribe Chrysitrichinae. Apparently, Koyama's decision was based only on the original description and not examination of the plant because in his article he described the spikelet as given by Pfeiffer.

Syntrinema and *Rhynchospora* are not remotely related. The inflorescence of *Rhynchospora* is composed of true flowers in true spikelets while that of *Syntrinema* is composed of pseudanthia in pseudospikelets. *Syntrinema* is an autonomous and distinctive genus. Although it has pseudanthia, these are so unusual that the genus should not be placed in the Mapanieae, not even in a separate subtribe, but in a new tribe, Syntrinemeae. Its differences from the Mapanieae are:

1. In the Mapanieae, each pseudospikelet is a visibly separate unit, even in those species of *Mapania* where they bunch together into a congested terminal inflorescence, and in *Chrysithrix* where the pseudospikelet is reduced to a single pseudanthium. In *Syntrinema* the pseudospikelets borne on a culm are united into a single dense spicate head in which the individual pseudospikelets cannot be distinguished without dissection.
2. The size and habit of the plant are completely different from almost all species of Mapanieae.
3. The glumellas are in the form of bristles, not laminas as in all Mapanieae.
4. Two lower, lateral, folded glumellas occur in all Mapanieae except *Chrysithrix*. In *Chorizandra* they occur but are not folded so strongly nor is the whole midvein ciliate (according to Clarke's drawing in Tab. CXIX). *Syntrinema* does not possess these lateral, longitudinally folded glumellas.
5. In the Mapanieae there is only one kind of pseudanthium, which is bisexual. In *Syntrinema* there are three kinds, one bisexual, one male or possibly neutral, and the third male.

Syntrinemeae L. T. Eiten, trib. nov.

Inflorescentia capitulum unicum pseudospiculis spicata dispositis; quaeque pseudospicula prophyllo et bractea inferiore vacuis et ca. 9–10 pseudanthiis spicate dispositis in axillis bractearum glumiformium obsita; 2 pseudanthia inferiora bisexualia, quidque 3 floribus masculinis unistaminatis lateralibus in axillis glumellarum setiformium et flore femineo terminali (aut pseudoterminali?) cum pistilo unico et 3 glumellis setiformibus hypogynis; 2 pseudanthia sequentia masculina (neutra?), quidque 1–2 floribus masculinis lateralibus unistaminatis (aut staminodiis?) in axillis glumellarum setiformium; cetera pseudanthia quidque 3 floribus masculinis unistaminatis; in hoc pseudanthio 3 filamenta in columna connata et 3 antheris liberis, rachilla et glumellae setiformes non separate visibilis, aut carentes aut adsunt et cum columna filamentorum connatae.

A tribu Mapanieae differt: pseudospiculae in capitulis aggregatae; pseudanthia masculina ac bisexualia adsunt; glumellae setiformes. A tribu nova Micropapyreae differt: pseudospiculae in capitulis aggregatae; pseudanthia masculina ac bisexualia adsunt.

Type genus: *Syntrinema* Pfeiffer, Repert. Spec. Nov. Regni Veg. 21: 238. 1925.

I hereby designate the sheet of *Luetzelburg 15484*, deposited in the Botanische Staatssammlung München (M), as lectotype of *Syntrinema brasiliense* Radlk. & Pfeiffer because it is the only one of the three cited syntype collections marked on the sheet as "Typus." I exclude as part of the lectotype the fragments of *Chorizandra* in the envelope glued to this sheet.

Chamaegyne pygmaea Suessenguth
HOLOTYPUS
det. Liene Teixeira Filen, 1975

HERBARIUM MONACENSE
Brasilianische Grenzexpeditionen General Rondon
Nr. 21041.
Chamaegyne pygmaea Suessenguth
Determ.: Suessenguth . 1941.
Nordbrasilien: Milho (wohl am Rio Tacutú Feuchter Camp. im Gebiet des Rio Branco (Am.)
Leg. Ph. v. Luetzelburg IX. 1927.

Chamaegyne pygmaea Süss.

(=*Eleocharis chamaegyne* L. T. Eiten)

Description of the holotype of *Chamaegyne pygmaea* Süss., Bot. Jahrb. Syst. 73: 114–115. 1943: Brasilia septentrionalis [Território de Roraima], Milho, prope Rio Tacutu, in ditione fluvii Rio Branco, in campo humido, Sep. 1927, *Luetzelburg 21041* (M).

The plant forms minute clumps (it is not known whether these were isolated or were pieces pulled out of a continuous mat) up to 3 cm tall (Fig. 22). The roots are abundant and vigorous in relation to the size of the plant. The mature culms are 5–25 mm long and 0.10–0.22 mm wide, triangular in cross section with each face depressed and forming an obtuse angle in its middle, light grayish green densely lined with purplish brown. At the base of each culm there is a triangular scalelike prophyll 1.2–3.5 mm long with two convergent veins (Fig. 23, a). Above the prophyll two leaf sheaths enclose the lower part of the culm; the lower sheath is external, 1.0–2.0 mm long, with a slightly wider apex of thin tissue and an oblique mouth (Fig. 29, b); the upper sheath is internal, 3.5–6.0 mm long, with a visibly wider or slightly inflated apex of thin tissue and an oblique mouth (Figs. 23, b; 29, c); this sheath is rose-purple, becoming lighter around the mouth. When young the culm is completely included in the lower sheath (Figs. 23, d; 28, d).

The spikelets are of two kinds: solitary and terminal at the culm apices, and sessile at the base of the clump between the culm bases. The spikelet at the culm apex is elliptic-oblong, flattened, (1.0–)1.5–1.6(–2.0) mm long and 0.2–0.3 mm wide. It has two subopposite, membranous, laterally folded glumelike bracts with the dorsal midvein greenish and streaked with purplish brown lines, and with the lateral portions hyaline with purple spots. Both of these laminas would usually be called glumes, but for reasons explained in the section on *Helonema*, I prefer to consider the lower one not part of the spikelet proper; it is therefore not to be called a glume but rather an associated scale. It surrounds the base of the upper lamina or true glume and never bears a flower. The true glume usually contains a male flower with 2–3 stamens (Figs. 30–34) or sometimes a bisexual flower consisting of a pistil and 1–2 stamens (Fig. 27). Rarely, the true glume is empty also.

When a culm does not have an apical spikelet, its apical meristem is covered by two scalelike subopposite bracts, the lower larger and surrounding the upper (Fig. 25). This lower bract is homologous with the associated scale on a culm tip bearing a spikelet; the upper bract is homologous with the lowest true glume, i.e., in 1-flowered spikelets such as in this species, with the single true glume. Sometimes the culm tip produces a vegetative shoot consisting of a whorllike short sympodial axis with a series of culms (Fig. 26). The first culm (Fig. 26, c)

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FIGURE 22. Holotype sheet of *Chamaegyne pygmaea* Süss. (= *Eleocharis chamaegyne* L. T. Eiten); *Luetzelburg 21041*; × 0.4. Each piece on this sheet was probably part of one mat. The following drawings of this species, Figs. 23–52, were made from plants of this sheet.

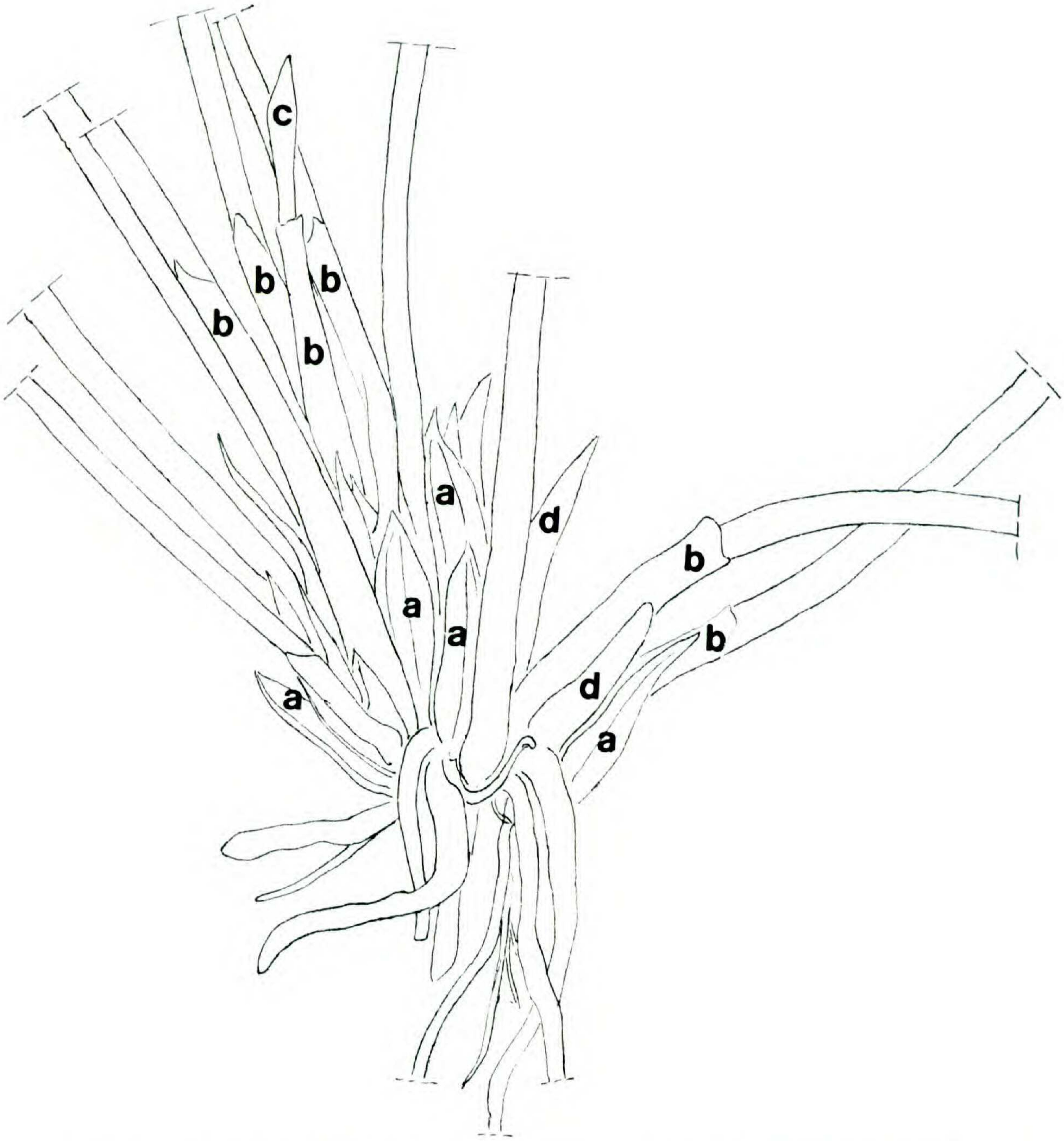
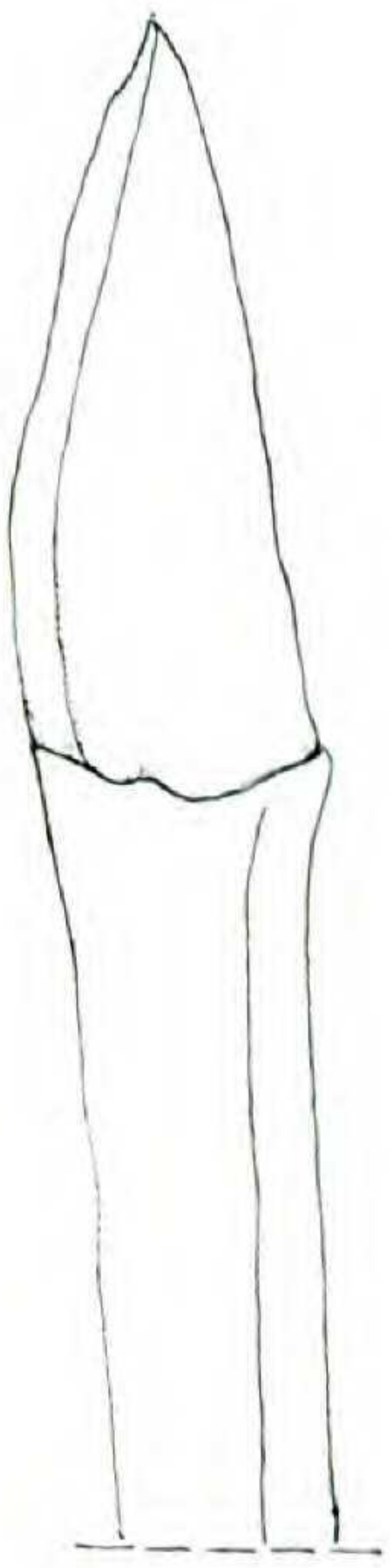


FIGURE 23. Base of clump without basal spikelets; × 23. a = prophylls; b = upper leaf sheaths; c = young culm with male spikelet; d = young culms still covered by their prophylls and sheaths.

of such a short shoot arises in the axil of the lower apical bract (Fig. 26, a). The second culm (Fig. 26, f) arises from the meristematic base of the first culm in the axil of one of the two leaf sheaths, penetrates the base of the sheath(s) and immediately emits a prophyll (Fig. 26, e). The third culm of the shoot arises from the base of the second culm and emits its prophyll, etc. A diagram of this branching is shown in Fig. 110.

The sessile spikelets at the base of the clump terminate very short axes which arise between the culms (Figs. 24, 35–38). This short axis has as its lowermost lateral organ a triangular prophyll with two convergent nerves (Figs. 37, a; 38, a; 40). Above the prophyll there are 1–2(–3)empty, wide, membranous scales with

FIGURE 24. Base of clump with basal spikelets; × 22. Note roots, base of culms (some with leaf sheaths visible), young basal spikelets with stigmas projecting from between glumes, and basal spikelets with mature fruits.



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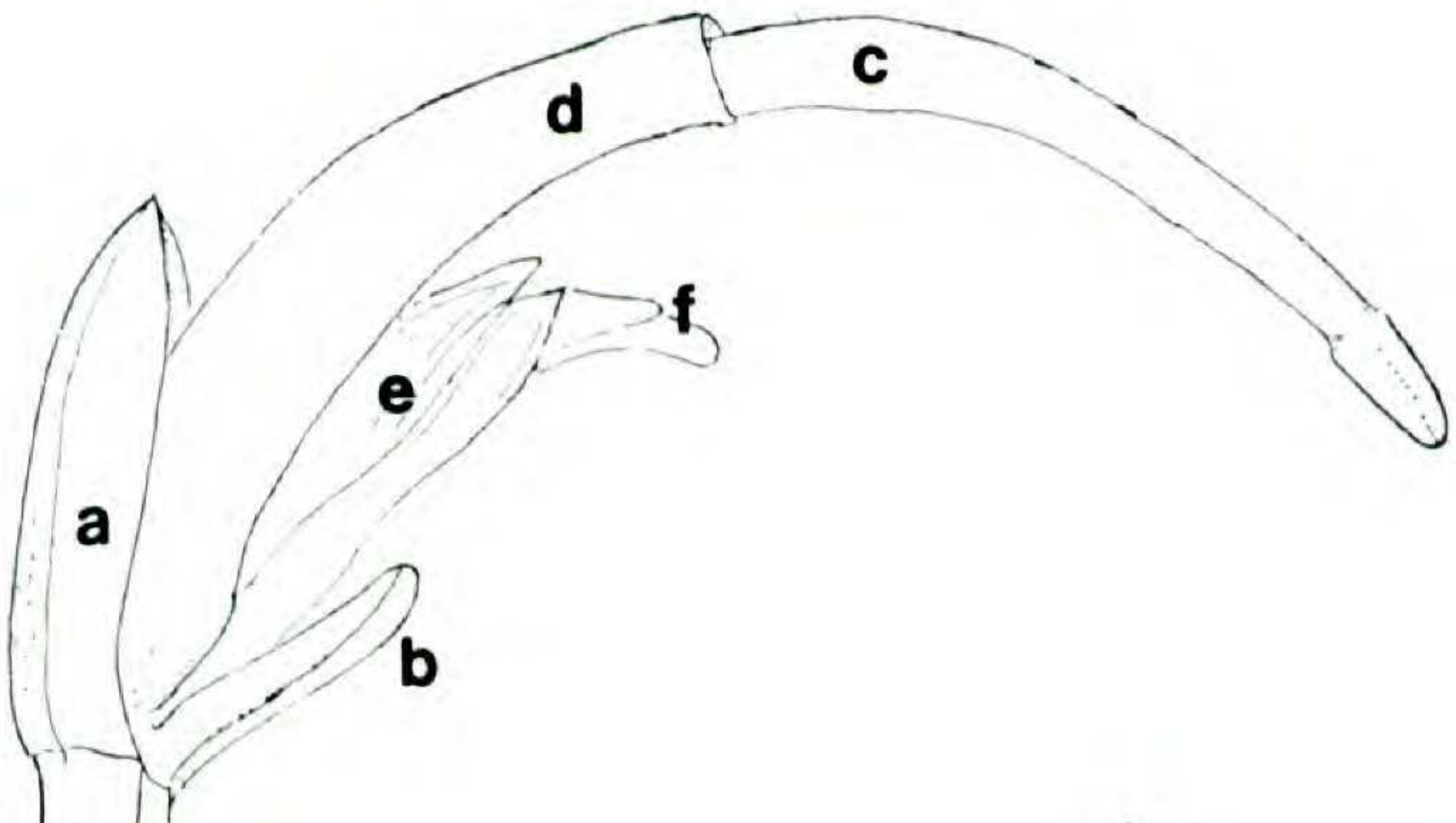

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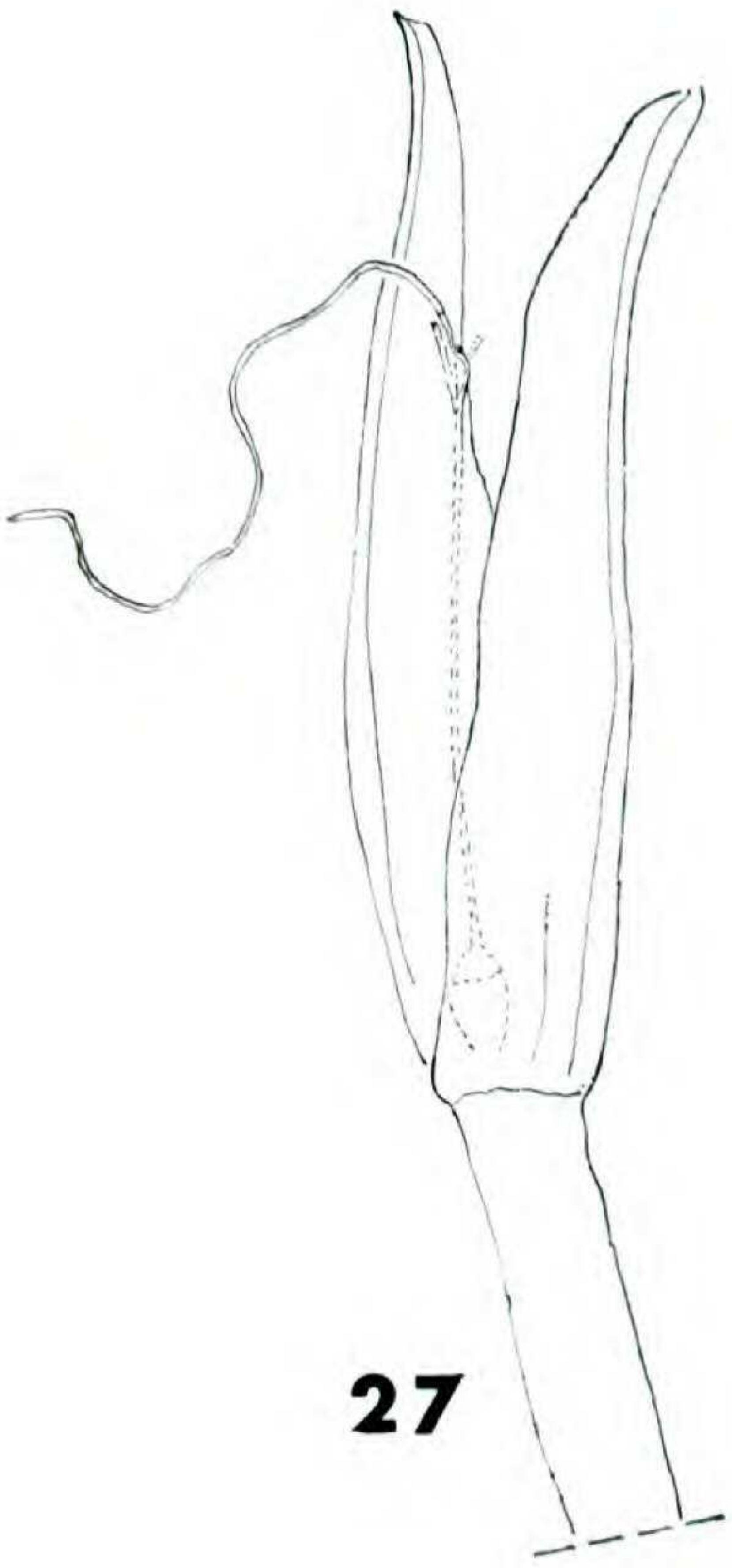

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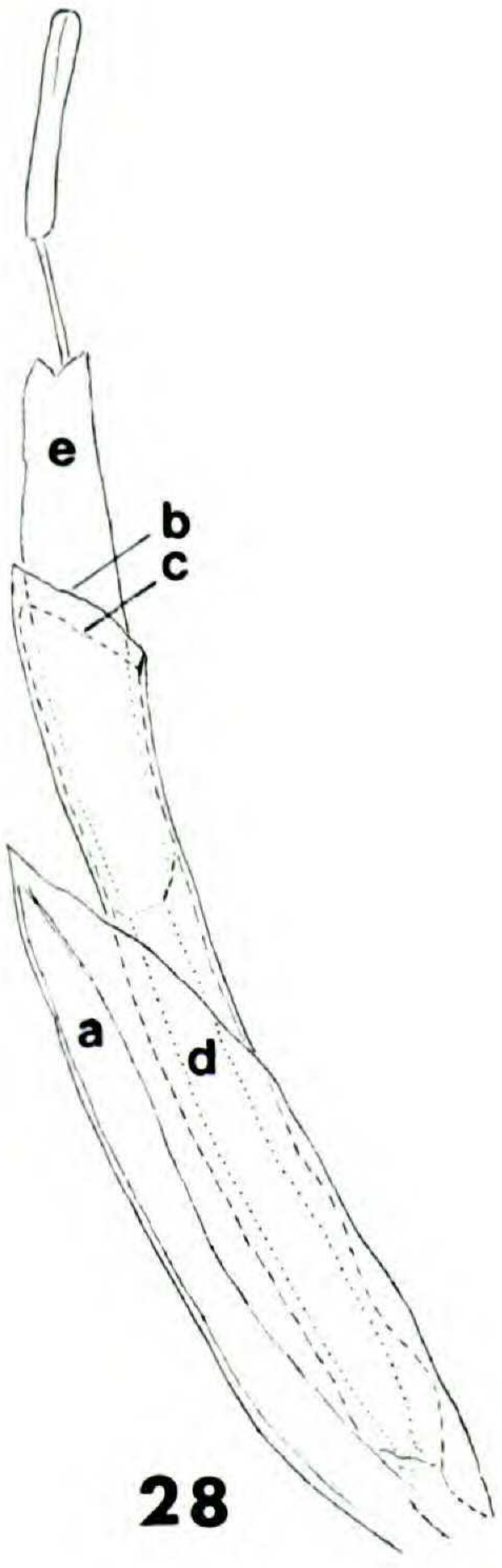

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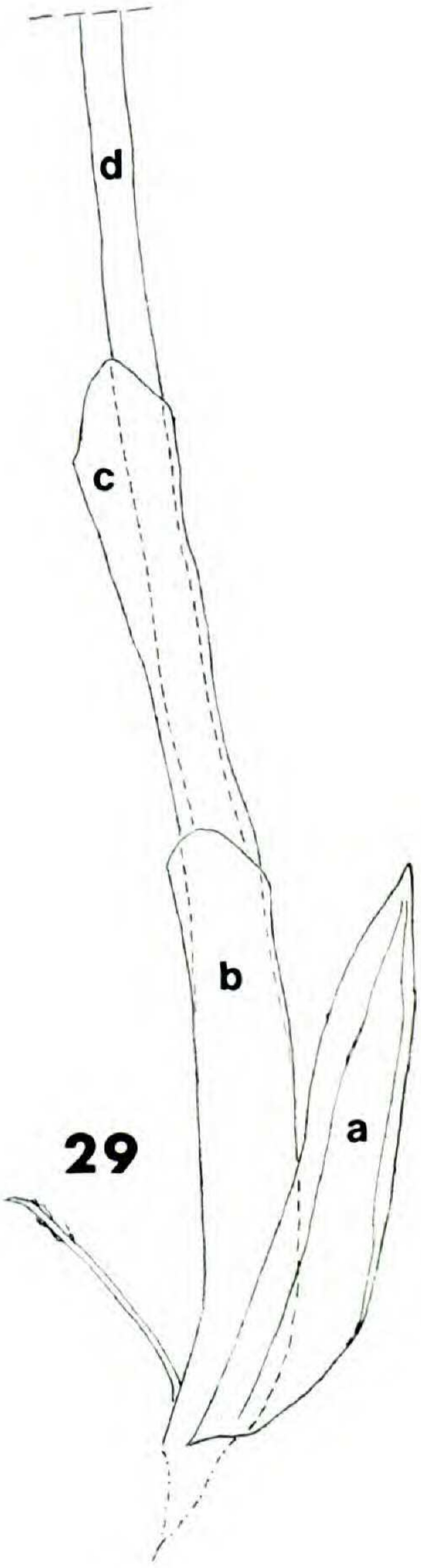

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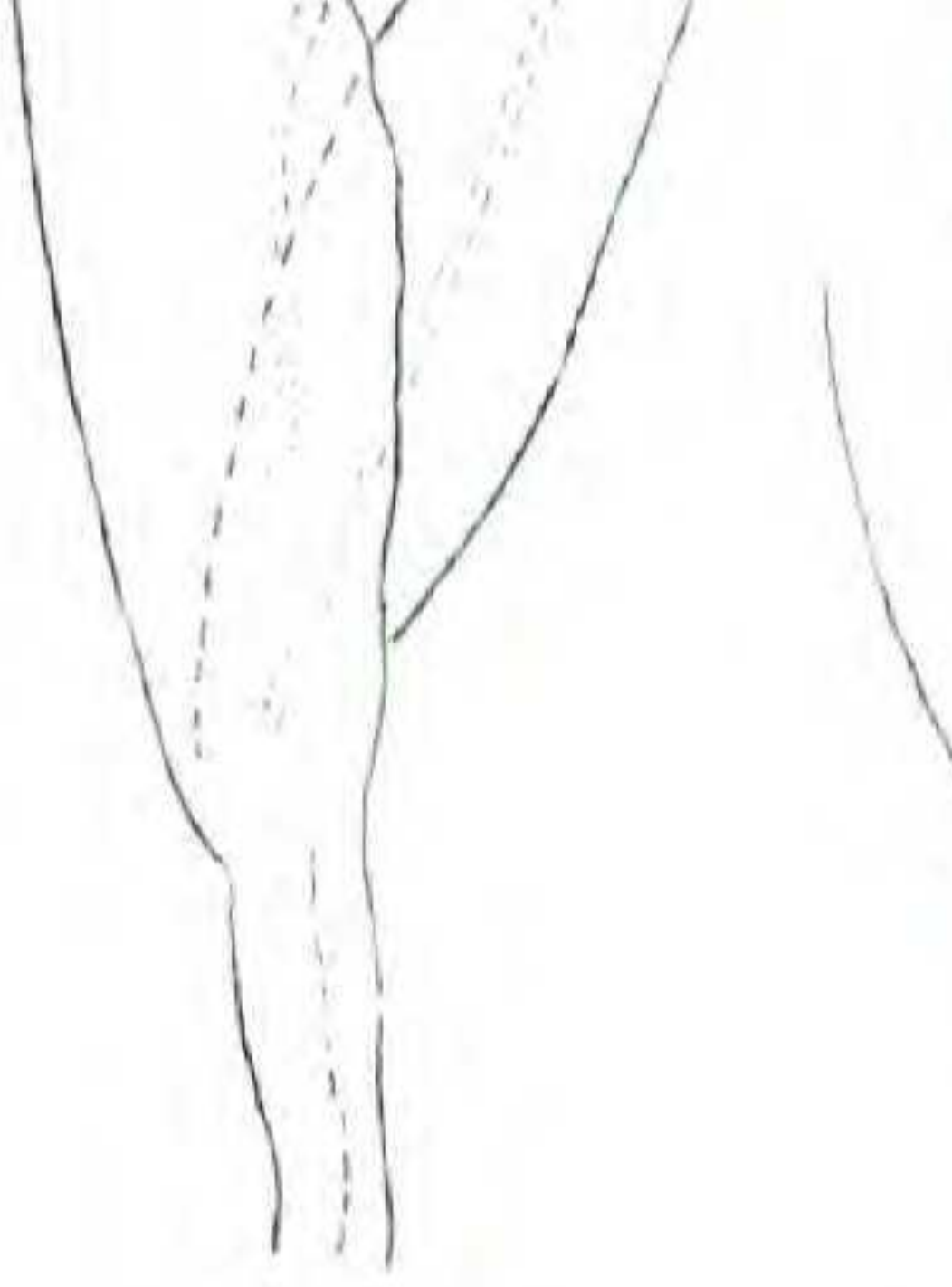

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an obtuse or rounded apex and with one midvein which is slightly visible or not visible (Figs. 35–37, b, c, d; 38, b; 39). At the tip of the axis are two longer subopposite laminas. The lower is the associated scale (Figs. 35–37, e; 38, c; 41) and the upper is the true glume (Figs. 35–37, f; 38, d; 42). The associated scale and the glume are lanceolate, membranous, 1.8–2.8 mm long and with a purple median stripe on the dorsal surface. The associated scale is always empty and surrounds the base of the glume, which contains the flower. Besides these parts, the short axis sometimes has another wide short scale just above the prophyll; in the axil of this scale there is a stem rudiment with a basal ligule (Fig. 37, b). In other short axes, this extra scale is lacking but in the axil of the prophyll there is a vegetative formation consisting of two tubular membranes like the fingers of a glove, the lower containing the upper and both covering a meristematic point (Fig. 43, b).

In the basal spikelets the flowers are female (Figs. 43–44) or bisexual (Figs. 45–48); in the latter, 1–2 stamens accompany the pistil. The stamens have hyaline filaments and golden-yellow anthers. The pistil is trigonous with a separately marked-off stylebase, a trigonous style, and three stigmatic branches with short transparent hairs (Fig. 49).

The mature achene has a globose-trigonous body 0.7–0.9 mm tall (not counting the stylebase) and 0.6–0.7 mm wide; the surface is cancellate (with large rectangular depressions in vertical files) and dull ivory-white. The stylebase is pyramidal, 0.15–0.25 mm tall, 0.3 mm wide, and dull dark brown (Figs. 50–52).

There exists a short note by Süssenguth (1952) on an unpublished anatomical investigation of *Chamaegyne* made by L. Bittl which is preserved in the Munich herbarium.

Süssenguth (1943) thought that *Luetzelburg 21041* is related to *Eleocharis* by its similarity in habit, form of stylebase, and presence of leaf sheaths at the

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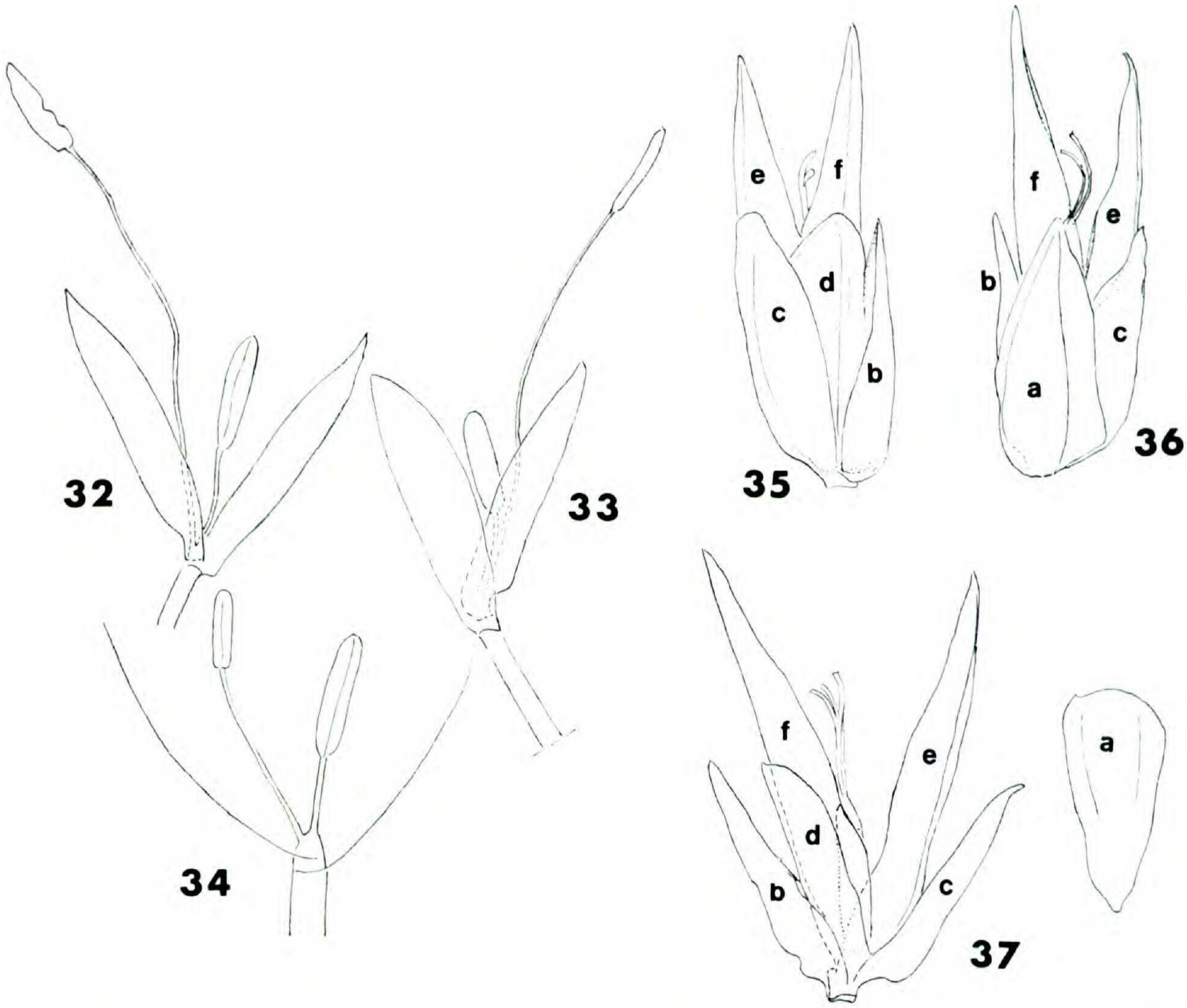
FIGURES 25–31.—25. Culm tip; × 66. Lower enrolled bract with margin visible. This bract totally covers the upper bract; both surround the meristematic culm tip.—26. Culm tip with young shoot; × 27. a = lower external bract at base of shoot; b = upper external bract at base of shoot; c = young culm arising from axil of bract a; d = upper or internal leaf sheath (the lower was not visible and is not shown); e = prophyll at base of the very young culm f; f = young culm still covered by its leaf sheaths. The lower bract, a, is homologous with the associated scale on a culm tip bearing a spikelet; the upper bract, b, is homologous with the single true glume of a spikelet.—27. Culm tip with terminal spikelet; × 43. Associated scale on right, glume subtending bisexual flower on left; filament from which anther has fallen extends to left.—28. Very young culm; × 13.6. a = prophyll; b = lower leaf sheath; c = upper leaf sheath (shown in dashed outline) still completely within lower sheath; d = culm (shown in dotted outline) still enclosed in its leaf sheaths; e = male spikelet. Even though the culm itself is just starting to lengthen, the filament of its spikelet flower is lengthening preparatory to anthesis.—29. Base of culm which bears a male spikelet; × 13.6. a = prophyll with two convergent veins; b = lower leaf sheath; c = upper leaf sheath; d = lower part of culm. In Figs. 28 and 29 the prophyll at the base of the axis is the prophyll of that axis and not the prophyll of a new axis that arises from it. This is because the ventral surface of the prophyll is turned towards the axis and not addorsed to it.—30. Culm-tip spikelet with male flower with three stamens, one still with its anther; × 16.5.—31. Semidiagrammatic representation of spikelet in Fig. 30. The apparently terminal male flower is really lateral (i.e., pseudoterminal) and arises in the axil of the glume (the upper lamina).



Figures 32–37.—32–33. Two views of a male spikelet at a culm tip; × 12.5. Note the associated scale and the glume arising at different levels and the flower with two stamens. The lengthening of the filaments is not synchronous.—34. Semidiagrammatic representation of this spikelet showing the pseudoterminal position of the flower.—35–36. Short axis with basal spikelet; × 28. Two views with parts in natural position. a = prophyll; b–d = scales; e = associated scale; f = glume with female flower (pistil).—37. Same spikelet with parts spread out; × 28. The small body in the axil of scale b is a branch from the rachilla which bears a ligule and meristematic rudiment not visible in this drawing.

base of the culms. However, he kept this species out of *Eleocharis* for two reasons: lack of a "perianth," i.e., bristles, and because the flowers are solitary (Einzelblüten), that is, not in spikelets. By Süssenguth's definition, a spikelet has to have more than one flower. Therefore, he set up the new genus *Chamaegyne*. But these two reasons are not really valid. In *Eleocharis*, bristles are not always present. There are species in which some individual plants have bristles with the achenes and others not. Frequently, on the same plant, young flowers do not show bristles while mature flowers and achenes show them. As for the "solitary flowers," that is, 1-flowered spikelets, these also occur in *Eleocharis*. There are species such as *E. minima* Kunth, whose apical spikelets usually have many to few flowers, but sometimes, even in good growing conditions, produce some 1-flowered spikelets, with only an associated scale ("empty glume") and the one true glume which subtends and encloses the flower. The spikelets of *E.*

TABLE 1. Comparison of the lateral organs on the culm and short axis of *Eleocharis chamaegyne* L. T. Eiten.

Culm	Short Axis
1 prophyll (scale with 2 convergent veins)	1 prophyll (scale with 2 convergent veins)
2 sheaths (with a midvein slightly or not visible)	1–2(–3) short wide scales (with a midvein slightly or not visible)
1 empty glumelike lanceolate associated scale	1 empty glumelike lanceolate associated scale
1 lanceolate glume with flower (rarely empty)	1 lanceolate glume with flower
male flower (rarely bisexual)	bisexual flower (sometimes female)

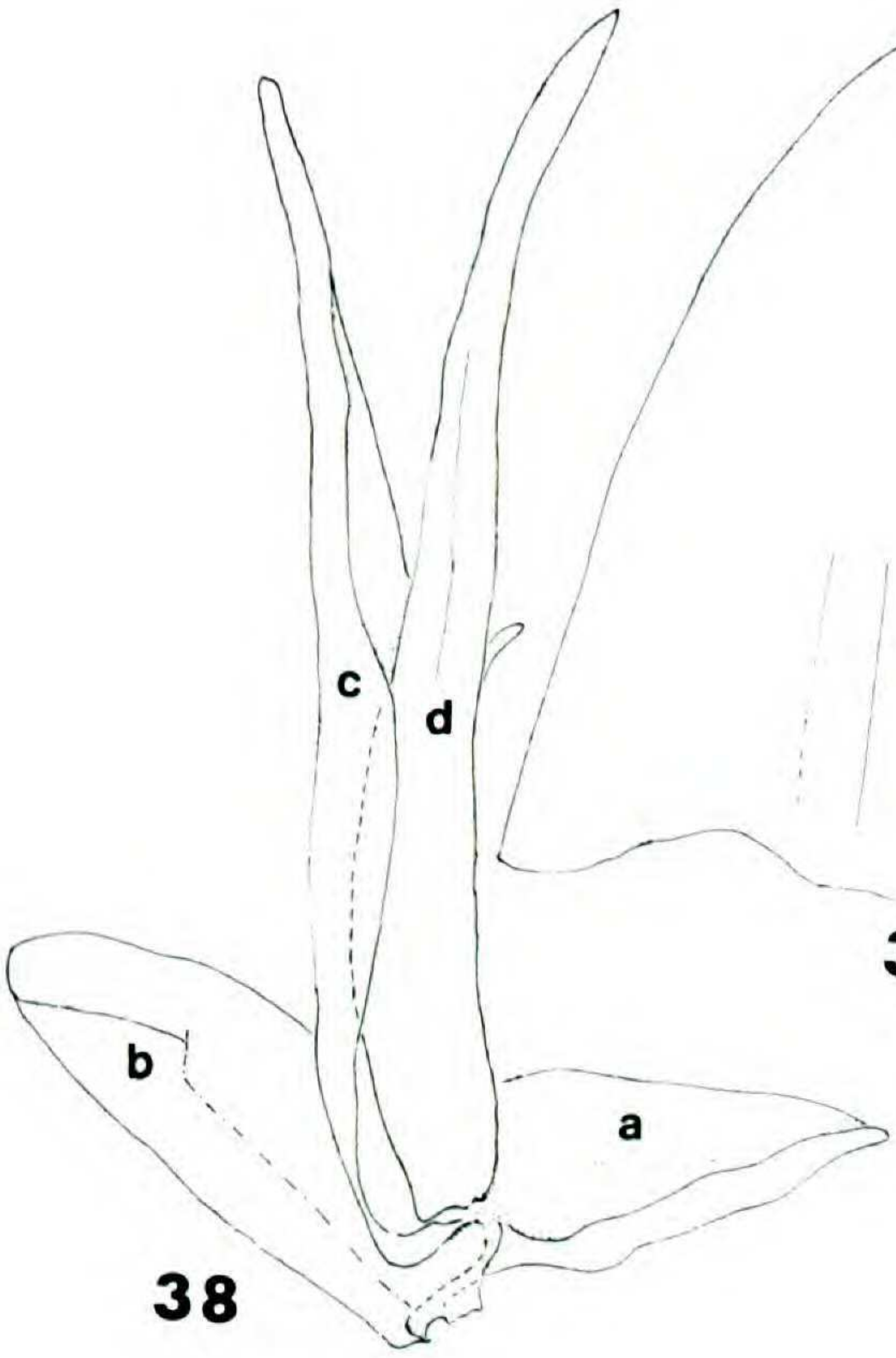
capillacea Kunth are 1-flowered with an associated scale and the glume which bears the flower. Rarely, in this species one can find spikelets with two or even with three flowers. In *E. naumanniana* Boeck. the apical spikelets are always 1-flowered, with an associated scale and a flower-bearing glume.

When Süssenguth (1943) described *Chamaegyne*, he mentioned that the plant has a rosette of leaves, that is, leaf blades. He wrote, "Blüten sitzen einzeln zwischen den Blättchen an der Erde." He stated that four leaves surround the pistil in the basal spikelets and that they are "foliis normalibus nec bracteosis nec glumaceis." The presence in *Chamaegyne* of "normal leaves," that is, leaves with true blades, would be a sufficient reason for excluding it from *Eleocharis* but, strangely, Süssenguth does not mention this character in his argument for separation. However, the only organs to which he can be referring are the glume, the associated scale and the usual two short scales of the short axis. He describes the "leaves" as being "Cr. 2 mm longe, lanceolata, acuta, tenerrima, integra, glabra, aliquando subfalcata;" these are exactly the characteristics of the associated scale and glume of the basal spikelets. The drawing of *Chamaegyne* given by Süssenguth (1943: Abb. 1) shows a pistil and a fruit between laminas which are undoubtedly these organs. Since the mature fruits fall from the basal spikelets, leaving their glumes empty, these empty associated scales and glumes at the base of the clumps are the remaining "leaves" which he shows in his drawing not associated with pistils or fruits. The prophyll and 1–3 scales which also occur below the glume and associated scale and are only a third to a half as long are not shown in Süssenguth's drawing. These scales and glumes are not normal leaves but rather opened-out and transformed leaf sheaths.

There exists a homology between the lateral organs on the culms and those on the short axes which bear the basal spikelets (Table 1).

The spikelets of this species should be defined so as to include only the uppermost lamina, that is, the true glume, and the flower in its axil. In this way, the definition is uniform for spikelets on culm tips and on the short axes, since the number of short scales between the prophyll and the associated long scale varies.

Although usually I have found male 1-flowered spikelets on the tip of developed culms, sometimes the flower was bisexual and mature. Süssenguth also



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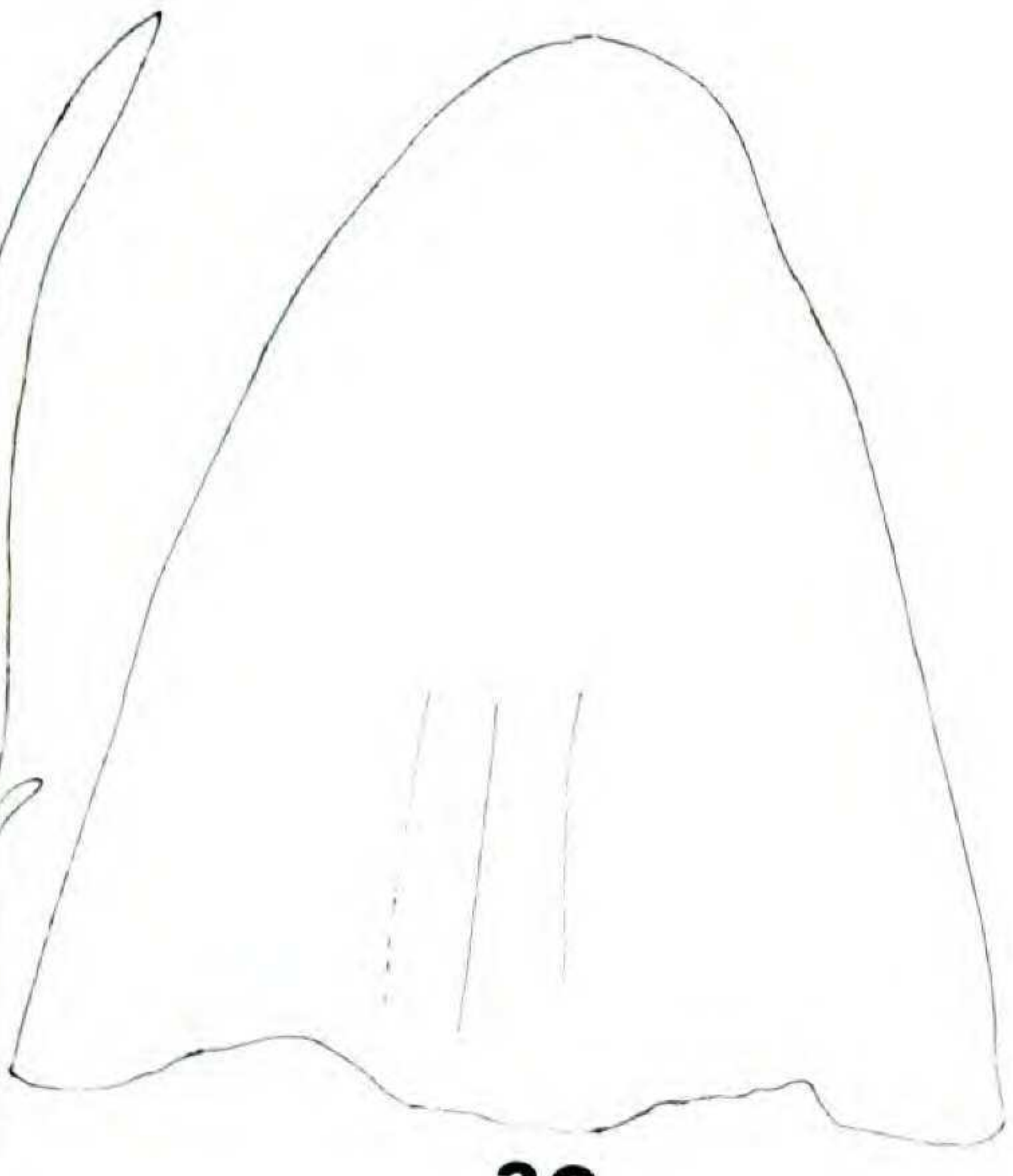

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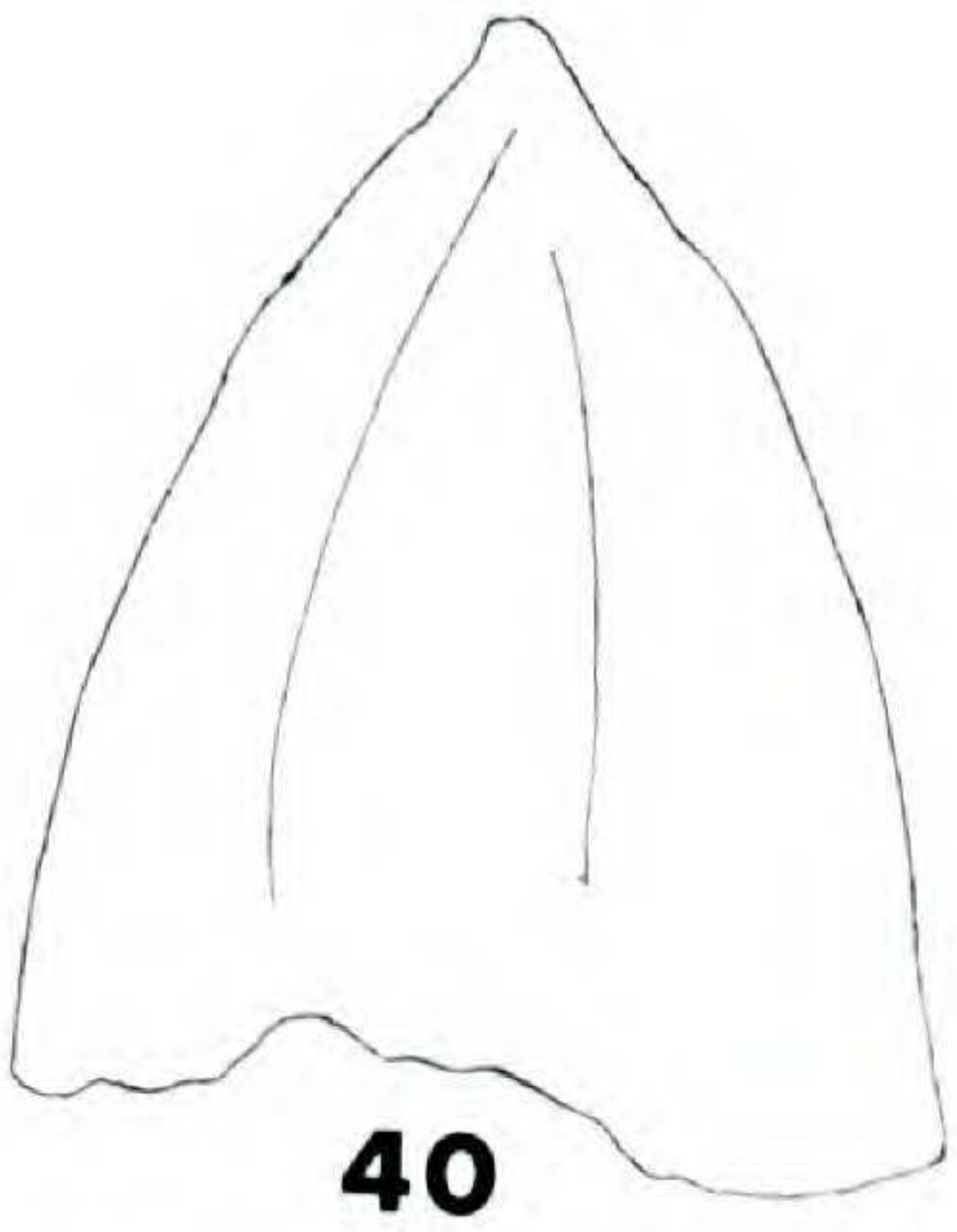

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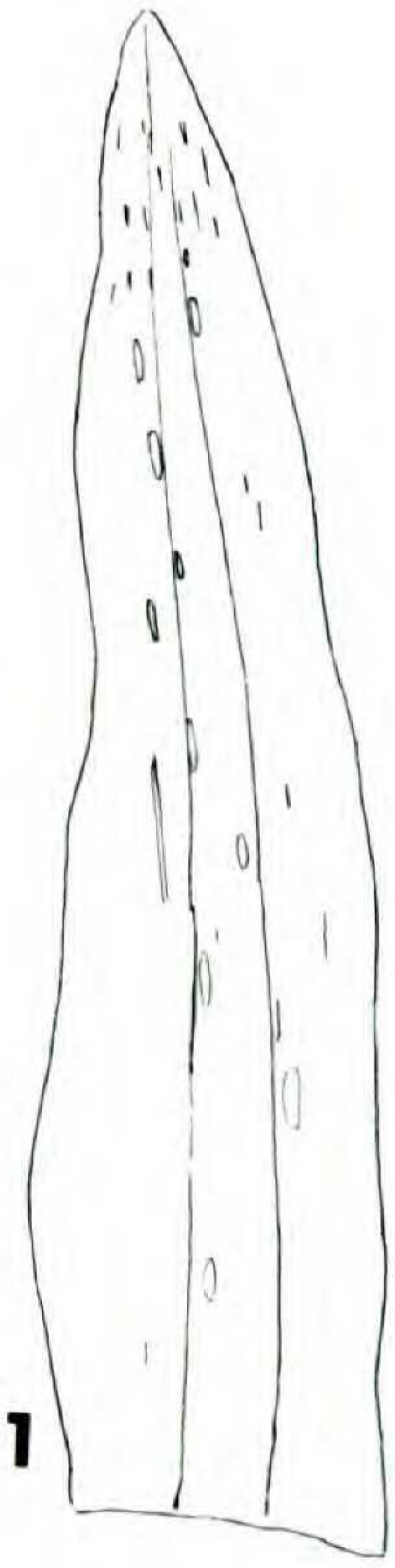

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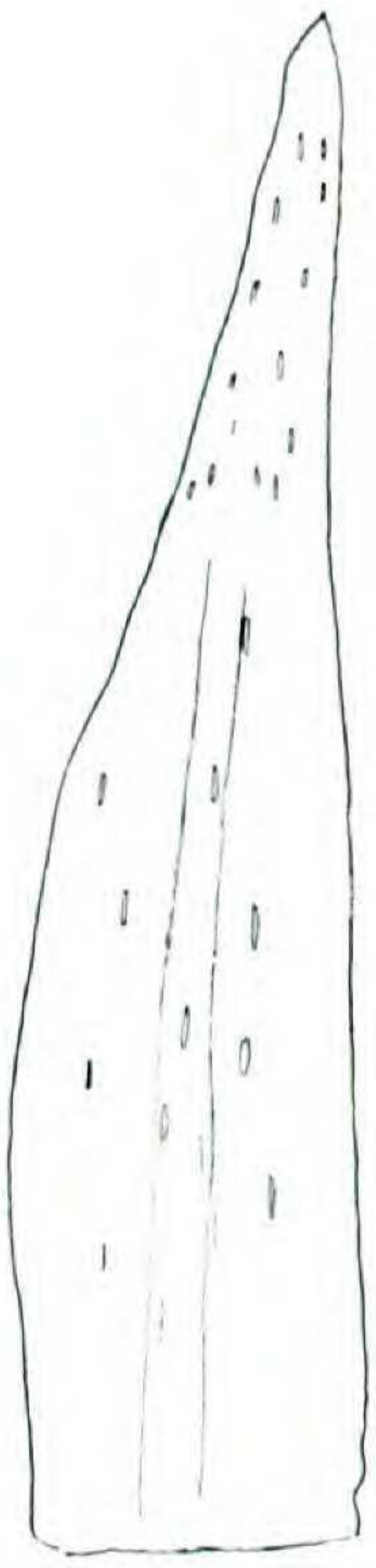

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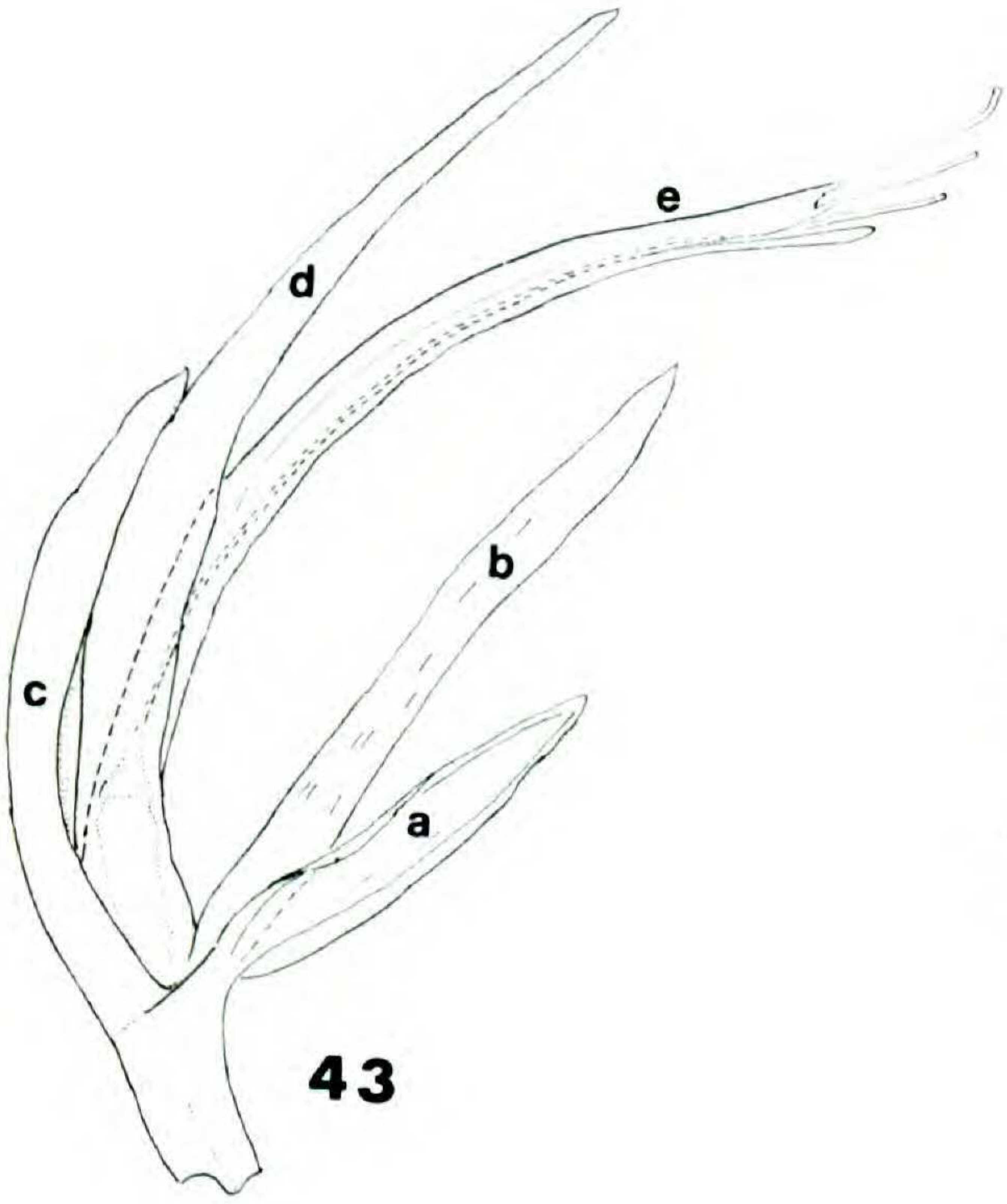

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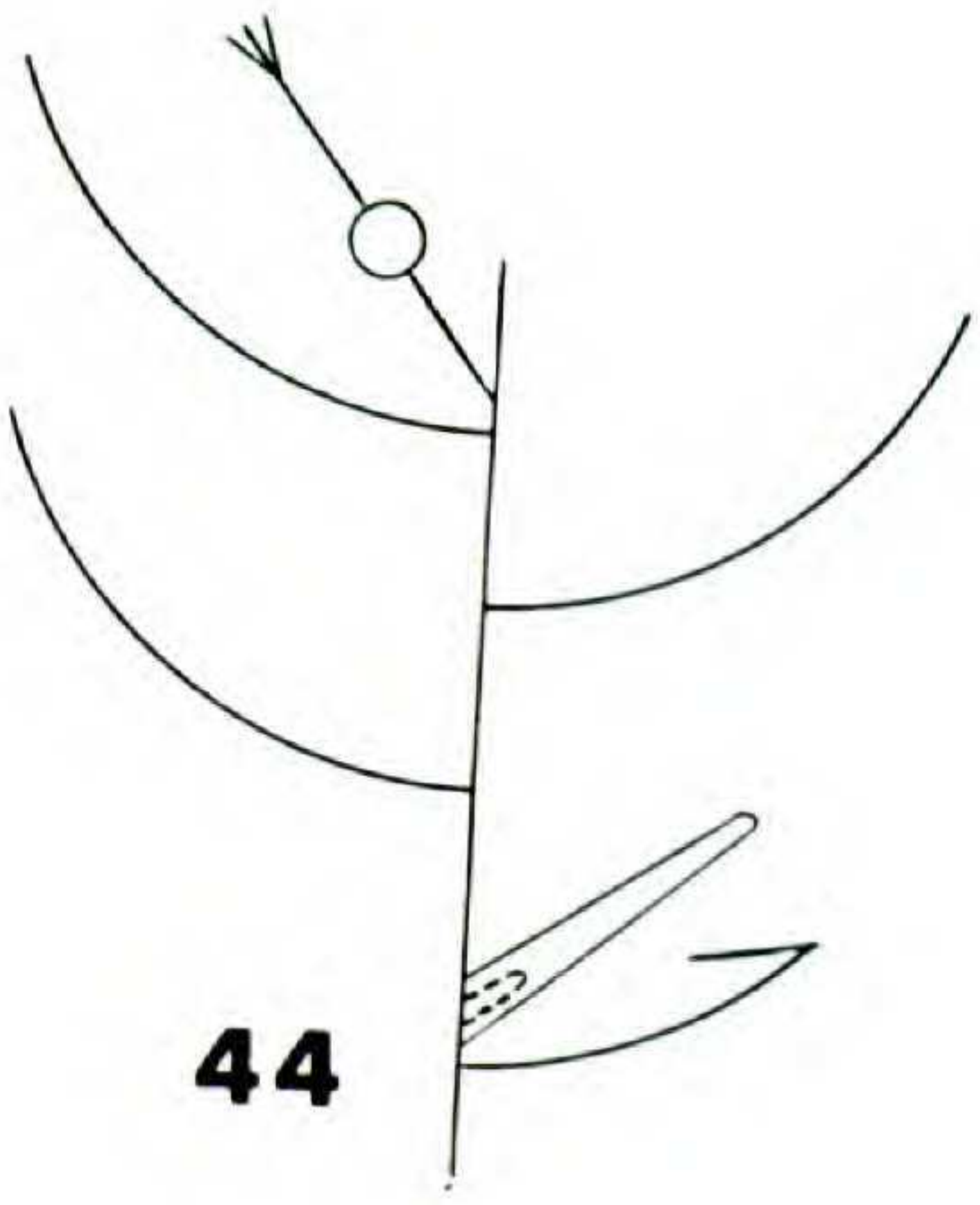

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Figures 38–44.—38. Short axis with basal spikelet with bisexual flower; × 40. a = prophyll; b = scale; c = associated scale; d = glume with flower. The prophyll and scale have been pulled down; part of the near side of the scale has been cut away to expose base of associated scale and glume.—39. Scale b flattened out, showing dorsal surface; × 60.—40.

found a young bisexual flower in a culm tip spikelet that had not yet grown out of its sheath, but he thought it was a teratological phenomenon ("aliquando in folio vaginali tubuloso, in quo scapis floris masculi expectatur, ovarium cum stylo etc., reperitur, quod autem nunquam maturescit et casum teratologicum offerre videtur"). The presence of bisexual flowers in the culm tip spikelets in *Chamaegyne* relates the species more closely to *Eleocharis* in which this is the usual condition.

The flowers which Süssenguth considered pseudobisexual because they possess stamens with twisted anthers ("mit einer verkummerten Anthere") are really ordinary bisexual flowers. The anthers become twisted in anthesis as is common in all Cyperaceae.

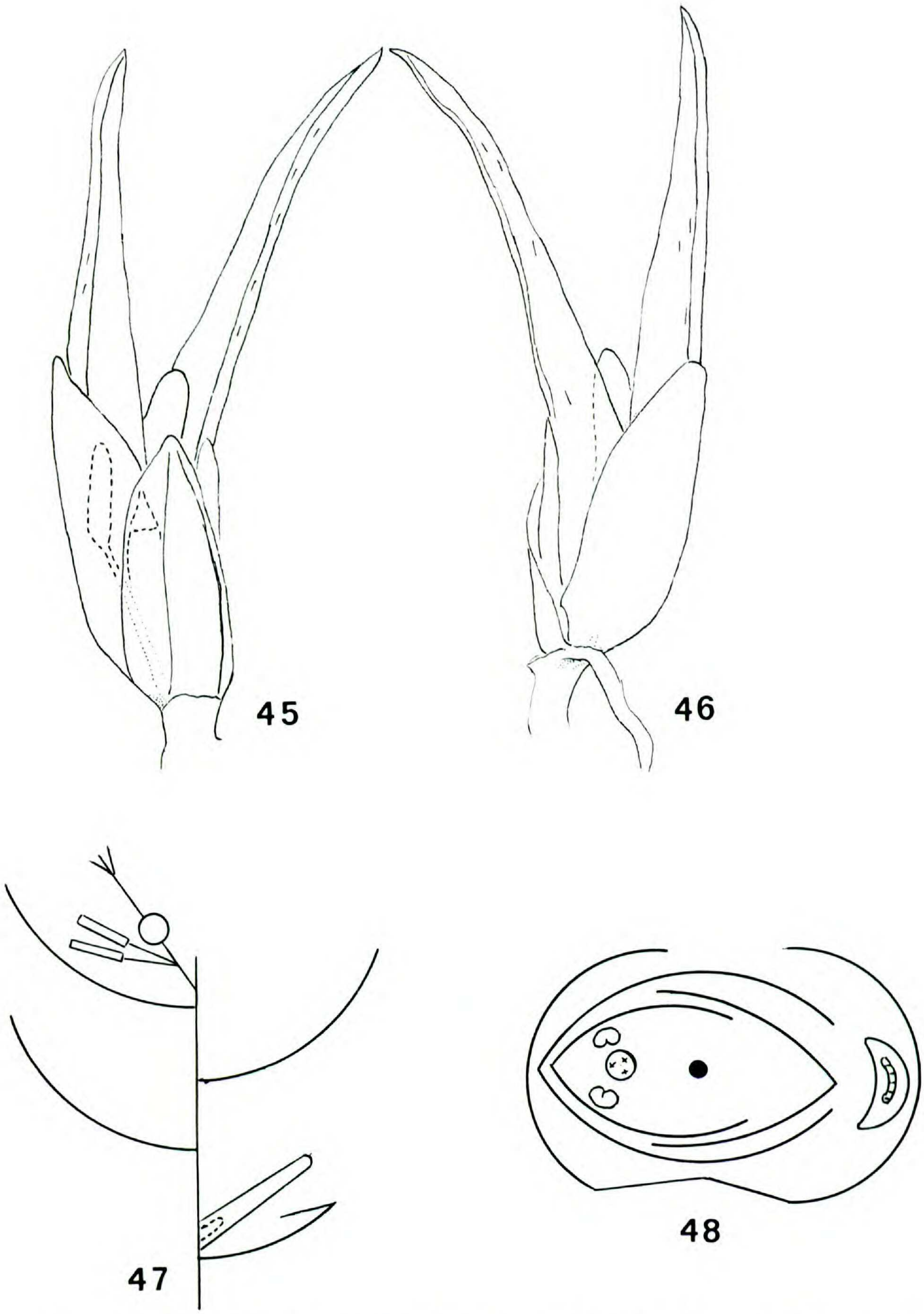
From this exposition there remains no character that really distinguishes *Chamaegyne* from *Eleocharis*. I am convinced that the material of *Chamaegyne* belongs to a species of *Eleocharis* series *Tenuissimae*. Svenson (1937: 212) says: "In the dwarf species of the *Tenuissimae*, and nowhere else in the genus, sessile basal spikelets are of frequent occurrence. These are found at the culm-bases, often so abundantly as to form scaly bulblike masses. Each spikelet is 1-flowered, developing a single achene which is usually a little larger than the achenes produced in the normal spikelets. . . . Similar basal spikelets have been described by Chermezon in three Madagascar species of *Scirpus*, ... Such spikelets, according to Chermezon, are perhaps the result of alternate immersion and emersion."

Within the series *Tenuissimae*, *Chamaegyne* seems to be related to *Eleocharis minima*. Svenson (1937) gives a drawing of the basal spikelets of this species in his Plate 465, Fig. 8, which is very similar to my drawing, Fig. 24, which was made before I noticed the relationship between these two species. Also, the apex of the leaf sheaths of both species is somewhat widened or even a little inflated.

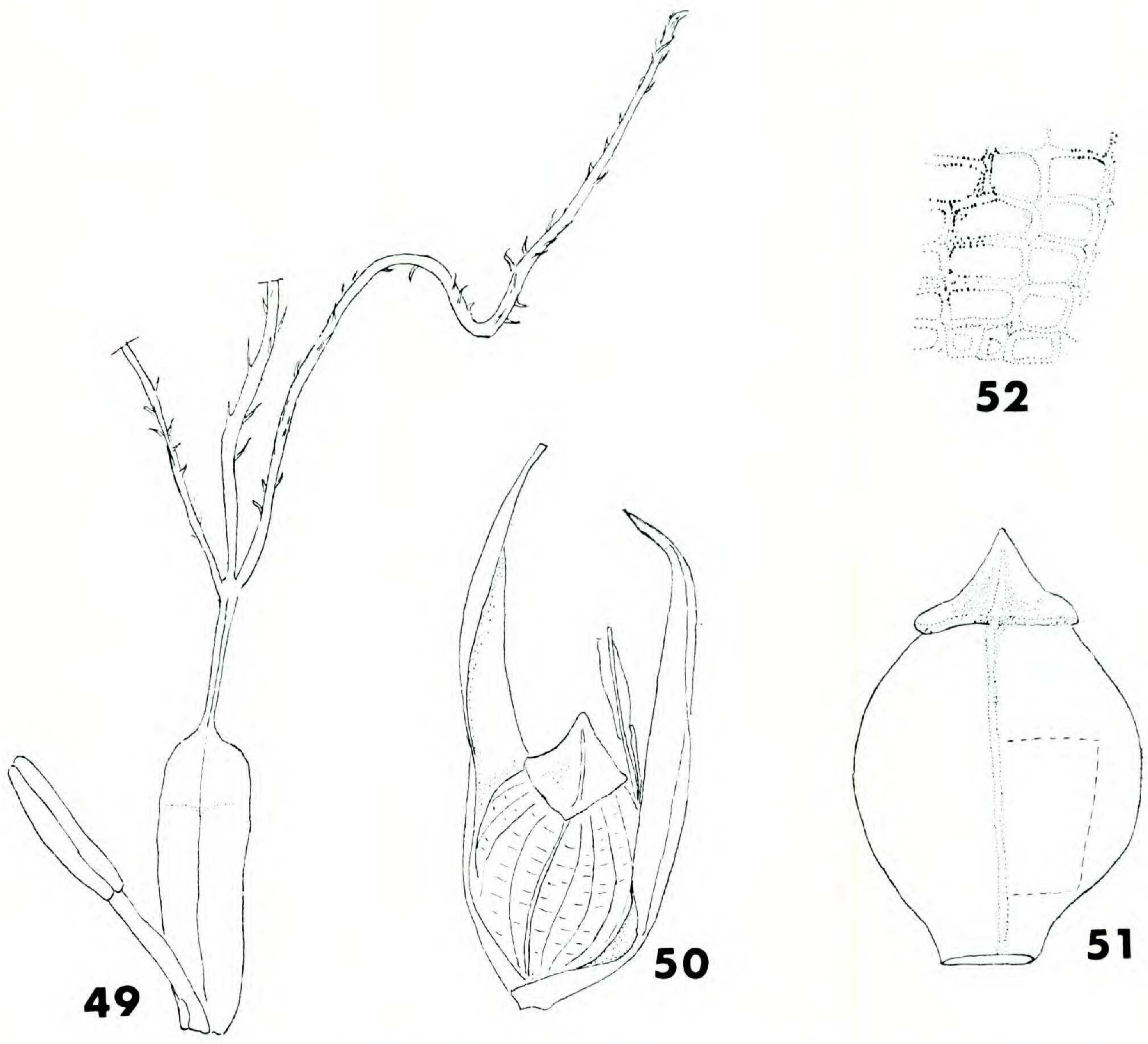
Despite these similarities, I believe *Chamaegyne* is a different species from *E. minima*. The principal difference is in the achene. *Eleocharis minima* has ellipsoidal-trigonous to obovoid-trigonous fruits which are 0.75–1.0 mm long (with stylebase), whitish to pale brown or olive, the surface marked with fine shallowly depressed rectangles with the long axis vertical. The achene of *Chamaegyne* is globose-trigonous, 0.85–1.1 mm long, dull ivory-white, the surface strongly cancellate with deep wide rectangles with the long axis horizontal (Fig. 52). The stylebase in *Chamaegyne* falls within the range of variation which this structure presents in *E. minima*.

In view of the difference in the fruits, organs of primary importance in separating species in *Eleocharis*, I consider *Chamaegyne pygmaea* as a new species. Its formal transfer was made in Eiten (1970: 273), where it was called *Eleocharis*

Prophyll flattened out, showing dorsal surface with two convergent veins; × 60.—41. Associated scale of a basal spikelet.—42. Glume. Both are flattened out and in dorsal view; × 40. Note vertical median thicker part and small elongated purplish brown streaks.—43. Short axis with basal female spikelet, the parts somewhat spread out; × 25. a = prophyll; b = tubular membrane (leaf sheath?) covering a meristematic rudiment (new culm?); c = empty short scale; d = empty associated scale; e = glume with pistil inside.—44. Branching pattern of this short axis.



FIGURES 45–48.—45–46. Two views of short axis with basal spikelet; × 38. Note prophyll, single short scale, long associated scale and glume. The tubular membrane in the axil of the prophyll is also shown. One of the stamens and the pistil in dotted outline is shown.—47. Branching pattern.—48. Floral diagram of this short axis.



FIGURES 49–52.—49. Flower from a basal spikelet; × 49. Young stamen with filament which has not yet elongated, and anther before anthesis. The oblong-trigonous ovary has a differentiated style base, trigonous style, and three stigmatic branches with short hairs.—50. Achene in basal spikelet between its associated scale and glume with remains of stamens; × 30. —51. Mature achene with conical stylebase; × 48.—52. Detail of the rectangular area in Fig. 51, showing cancellate surface; × 115.

pygmaea (Süss.) L. T. Eiten. Since there was a previously published *Eleocharis pygmaea* (Torrey, 1836: 313), it was renamed *Eleocharis chamaegyne* L. T. Eiten (Eiten, 1972).

Since *Chamaegyne* is therefore considered a species of *Eleocharis* and is obviously a reduced form of it, the single flower in its spikelet is not terminal as it appears but is pseudoterminal, that is, really lateral in the axil of its glume as are all flowers in *Eleocharis*.

Collections of other species examined (all det. L. T. Eiten) in connection with this study of *Chamaegyne*:

Eleocharis capillacea Kunth

BRAZIL: AMAZONAS: Manaus, margem do Igarapé do Cachoeira Alta, 10 Aug. 1955, *Chagas s.n.* (INPA, UB). GOIÁS: *Glaziou 22328*, ex herb. Schwacke (RB). DISTRITO FEDERAL: Catetinho, perto de Brasília, 25 May 1965, *Sucre 320* (UB). SÃO PAULO: São Paulo, Butantan, 5 Sep. 1917, *Hoehne s.n.* (SP). Mun. de Mogi-Mirim, 23 May 1927, *Hoehne 25190* (SP). Mun. de Mogi-Guaçu, Fazenda Campininha, 21 Apr. 1960, *Eiten & Eiten 1950-B* (SP). PARANÁ: Ponta Grossa, 15 Dec. 1903, *Dusén 2707* (R).

Eleocharis naumanniana Boeck.

LIBERIA. MONTSERRADO CO.: Bushrod Island, 19 Aug. 1949, *Baldwin Jr. 13021* (US). Ca. 20 mi E of Monrovia, 20 Aug. 1949, *Baldwin Jr. 13049 a & b* (US).

Eleocharis minima Kunth

Cited at the end of the section on *Helonema.*

HELONEMA ESTRELLENSE Süss.

(= *Eleocharis minima* Kunth)

Description of the syntypes of *Helonema estrellense* Süss., Bot. Jahrb. Syst. 73: 118–119. 1943: Staat Rio de Janeiro, Serra Estrella, in Rio Gongojoco, Oct. 1916, *Luetzelburg 14062* (M). Staat Rio de Janeiro, Serra dos Órgãos, Grota do Inferno, Wasserfall, an Granit im Wasser, Jan. 1916, *Luetzelburg 14027* (M).

The plant is delicate with capillary culms and a filamentous flaccid habit, forming numerous verticillate shoots (Figs. 53–54). The largest piece found was 25 cm long and had two orders of shoots. The shoots form on the apices of the culms (Figs. 60–61), and appear to arise from between two scalelike basal bracts. The lower of these external basal bracts of a shoot continues in the direction of the culm just below it and is 0.8–1.2 mm long and 0.5 mm wide (Fig. 66); the upper external basal bract is 0.4–0.8 mm long and 0.3–0.4 mm wide. Both bracts have a wide green stripe along the dorsal midvein and relatively narrow membranous sides. A shoot has 3–8 culms 7–10 cm long; each culm is associated with a bract at its base which is generally membranous. These bracts are often missing either because they possibly have not developed, or more probably, because they have decayed. They probably are prophylls.

Each culm has two basal tubular leaf sheaths which are made of extremely thin, more or less transparent tissue; the outer sheath is very much shorter than the inner (Fig. 67). Sometimes the sheaths are found with only short fragments of culm inside or they are completely empty. When empty, the sheaths in dry pressed material appear to be narrow, flat, thin leaf blades since the outer sheath is difficult to see and the walls of the inner sheath are glued to each other to form a flat lamina. Some culms (1–3) of a shoot bear new shoots at their tips made of 3–6 culms 1–3 cm long. At the base of the culms in a shoot, roots are commonly found. When a culm apex has neither a shoot nor a spikelet, the terminal meristem is covered by two small scalelike bracts; the lower is enrolled and oriented so as to continue the line of the culm; it grows beyond and encloses the smaller upper bract (Fig. 65). (In the fresh topotype material shown in Figs. 74–75, the two terminal bracts lie side by side.)

Vegetative multiplication by shoot formation at the culm tips and subsequent breaking of the older lower culms is the main method of reproduction of this plant when submersed. Spikelets form rarely, are very small and not evident. In the syntype material, the associated scale next to a spikelet (usually called the lowest glume by authors speaking about *Eleocharis*) always has a meristematic shoot of 1–2 culms in its axil (Figs. 55–57, 68, 70), or the shoot has grown into a young stage (Fig. 67), or it is well developed (Figs. 58, 63–64). In these shoots,

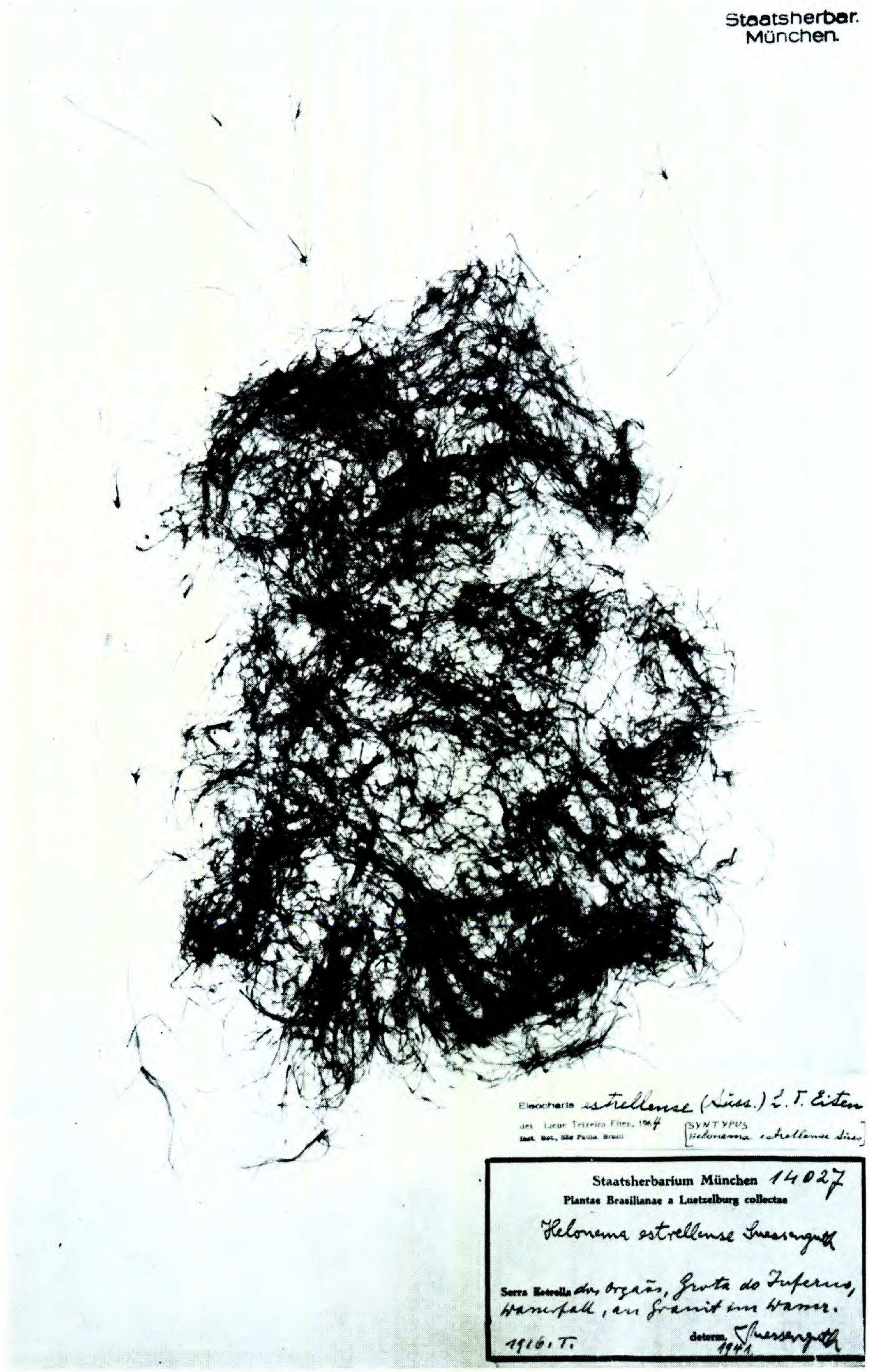


FIGURE 53. Syntype sheet of *Helonema estrellense* Süss. (= *Eleocharis minima* Kunth, extreme aquatic phase); *Luetzelburg 14027*; ×0.4. Figures 60–62 were made from material of this collection. The name shown in the annotation slip has since been changed.

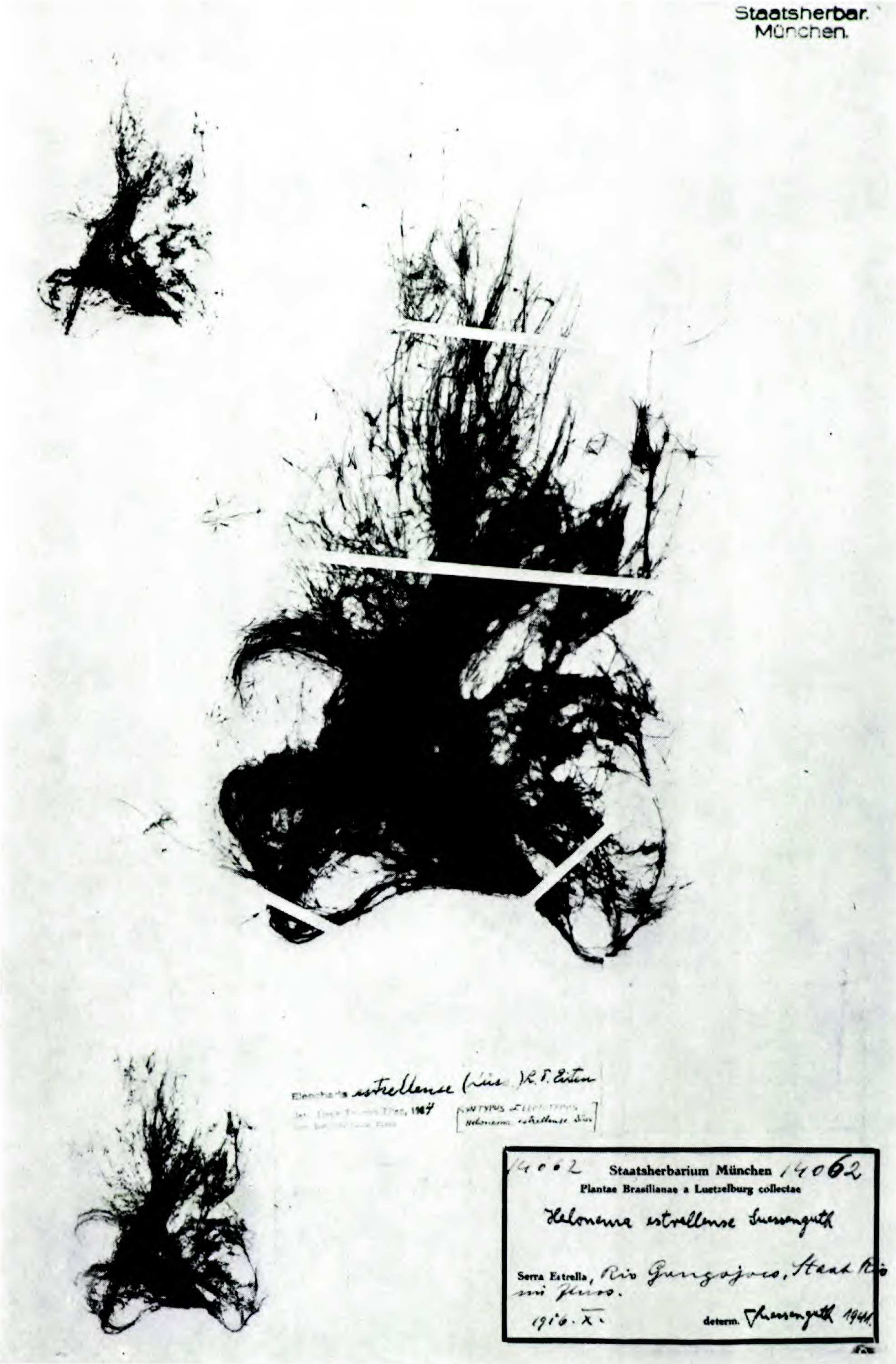


FIGURE 54. Lectotype sheet of *Helonema estrellense* Süss.; *Luetzelburg 14062*; × 0.4. Figures 55–59, 63–71 were made from material of this collection.

each culm arises from the base of a previously formed culm (branching pattern shown in Fig. 110). As in the basal shoots, a lamina is found associated with the base of some (Fig. 60) or all (Fig. 61) of the culms of a shoot. It is difficult to tell if these are prophylls, such as usually occur in *Eleocharis* clumps and culm tip shoots, or are opened-out lower leaf sheaths. Often no such scales are found among the culm bases (Figs. 58, 63) but whether they did not form in these cases, or formed and then decayed in the water, is difficult to tell from this material.

The spikelets are elliptical or oblong, flattened, 2.3 mm long and 0.6 mm wide. I exclude the associated scale ("lowest glume" of authors) and its axillary shoot

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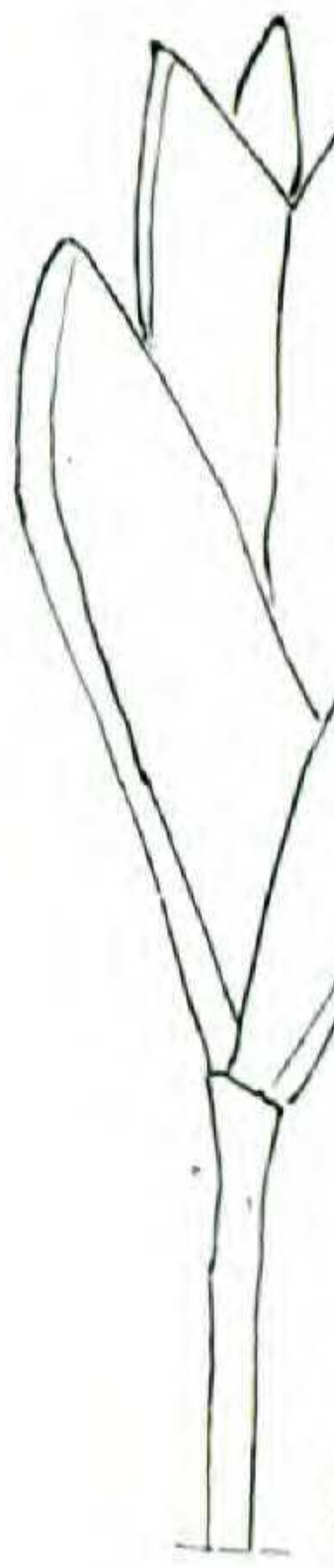
FIGURES 55–62. Spikelets, flowers, and shoots from the syntypes.—55. Spikelet with associated scale and four glumes; × 18.—56–57. Spikelets with associated scale and two glumes; × 18. Note tendency for distichous arrangement in these spikelets with a low number of glumes.—58. Culm apex showing association of spikelet and shoot; × 36. The shoot has two developed culms and a young one. The small projection at base of the left culm is a scar left by the associated scale. The prophylls of the second and third culms are not shown; they probably had decayed in the water. The lower leaf sheaths were not visible and so were not drawn.—59. Young bisexual flower taken from spikelet of Fig. 58; × 36. Note absence of bristles.—60. Base of shoot at culm apex; × 30. There is no associated spikelet here. Note the two external bracts at the base of the shoot, the lower, a, (next to root) and the smaller upper one, b. (The two vertical lines in a are the borders of a thickened middle portion that contains the midvein.) The shoot has four developed culms and a wide basal lamina, d, associated with one of the culms. The young culm, c, is still covered by its hood of leaf sheaths. The lower external bract of the shoot, a, subtends the oldest culm; the other culms arise successively from the meristematic base of a previous culm in the axil of the outer leaf sheath. The upper external bract, b, although at the base of the whorl, does not subtend any of the culms.—61. Shoot at culm apex, not associated with spikelet; × 30. The base of one of the culms of the shoot emits a root which leads off to the left. The shoot has two external bracts, a and b. The first culm, c, is developed and is associated with the large lamina, d, which is its lower leaf sheath split and spread out. The second culm, e, also developed, is associated with the lamina, f; the young third culm, h, is still contained in the hood of a leaf sheath, and associated with the lamina, g. Laminas f and g are probably also split and opened out lower leaf sheaths.—62. Diagram of cross section of shoot of Fig. 61. This shows the assumption that the laminas f and g of Fig. 61 are opened out lower leaf sheaths and that the prophylls belonging to the second and third culms of the shoot have rotted away and so are not shown. The shaded circles are culms and the circles around them represent their upper leaf sheath.

FIGURES 63–69.—63. Shoot of three culms at a culm tip, associated with a spikelet; × 40. The associated scale, the prophylls, and the leaf sheaths had decomposed.—64. Semidiagrammatic representation of the spikelet in Fig. 63, showing rachilla, glumes, and flowers. In the lower flower, the ovary and the base of the two filaments had fused, forming the thick body shown.—65. Apex of a culm which does not bear a shoot or a spikelet; × 40. The meristematic culm tip is covered by two scalelike bracts; the lower is larger and enrolled and covers the upper.—66. Lower of the two external bracts at the base of a culm-tip shoot, spread out, showing thick median portion; × 40.—67. Culm tip with shoot and spikelet; × 40. Shoot consisting of associated scale (equivalent to lower external bract) and two young culms. Spikelet with glumes spread out showing two basal male flowers of one stamen each and upper male flower of three stamens. The glume subtending the lowest flower was removed.—68. Culm-tip spikelet not associated with a shoot; × 40. The associated scale on right (partially disconnected) subtends the meristematic shoot rudiment shown in dashed outline in its axil. The other laminas are glumes and compose the spikelet proper. The glume at left subtends a male flower of one stamen (shown in dashed outline). Note prolongation of rachilla and second glume. This glume covers a third glume not shown.—69. Young flower with pistil and two stamens; × 40. (Anther of one of the stamens not shown.) Note absence of bristles.



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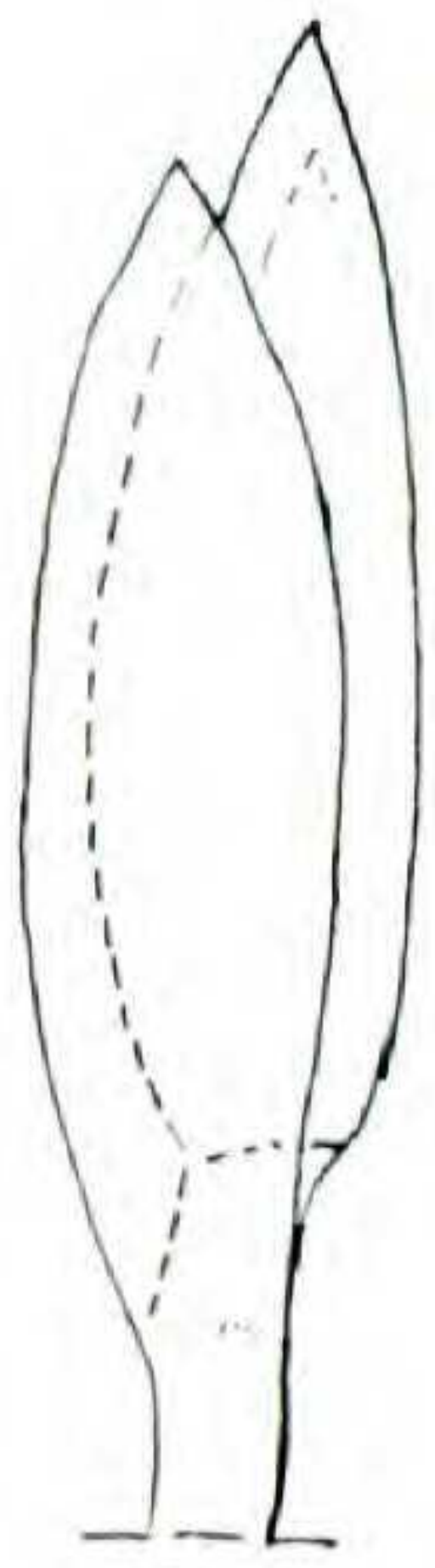

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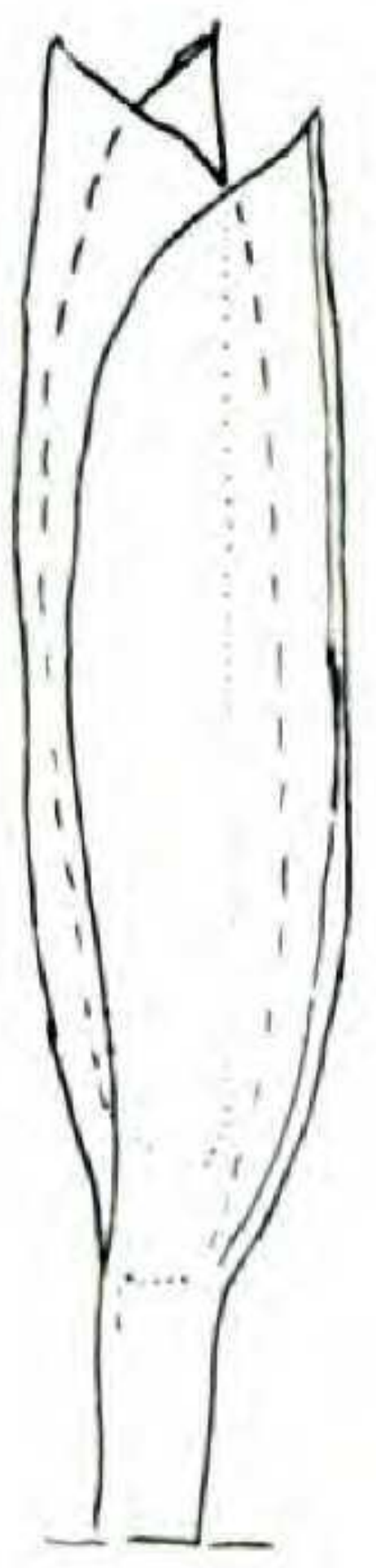

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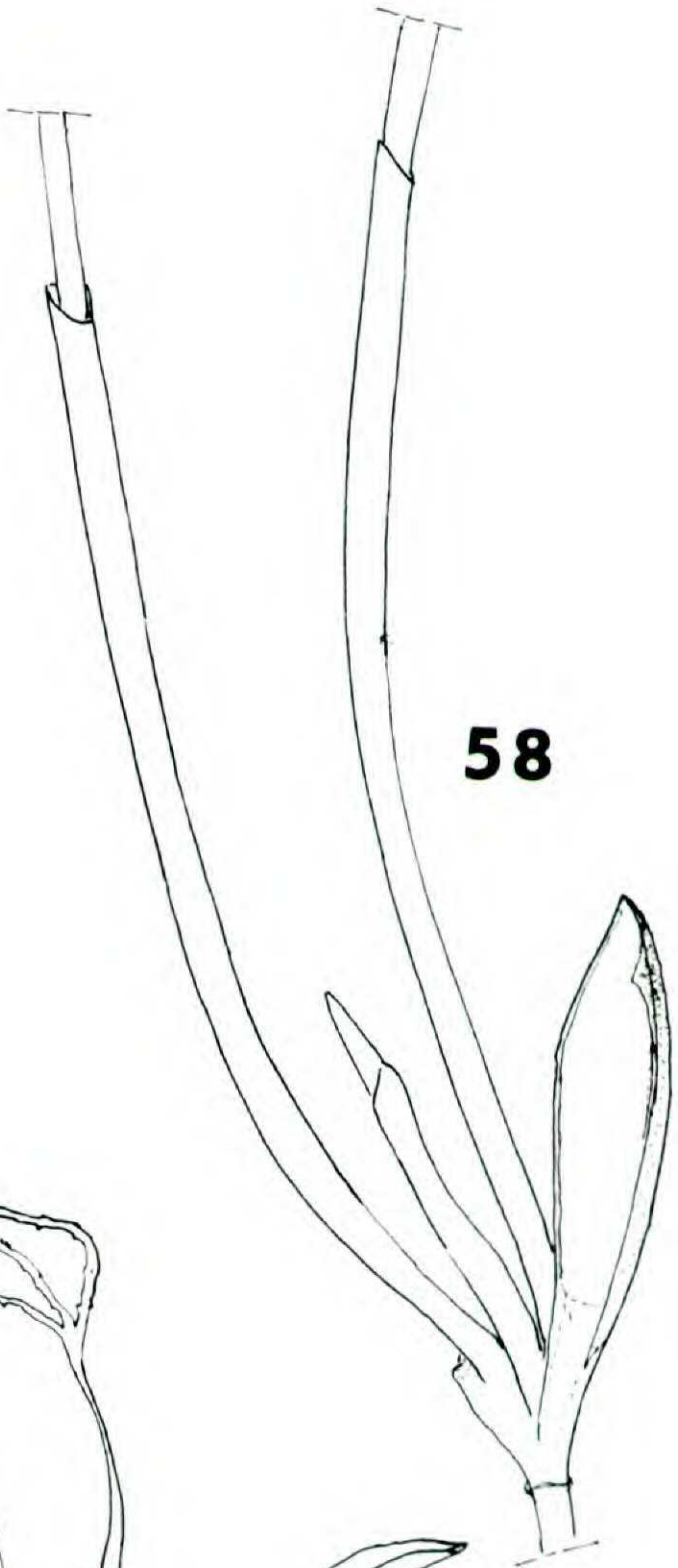

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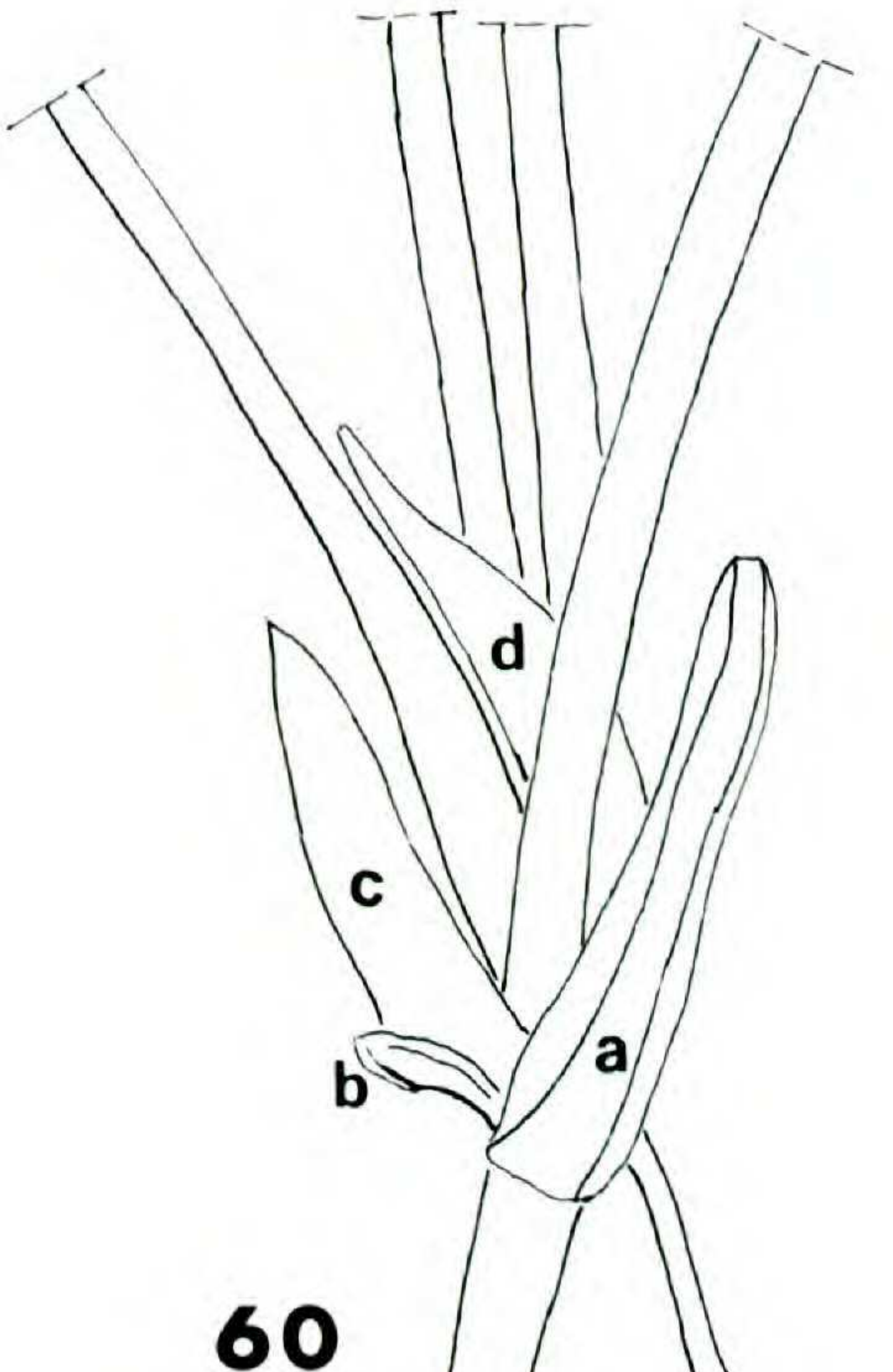

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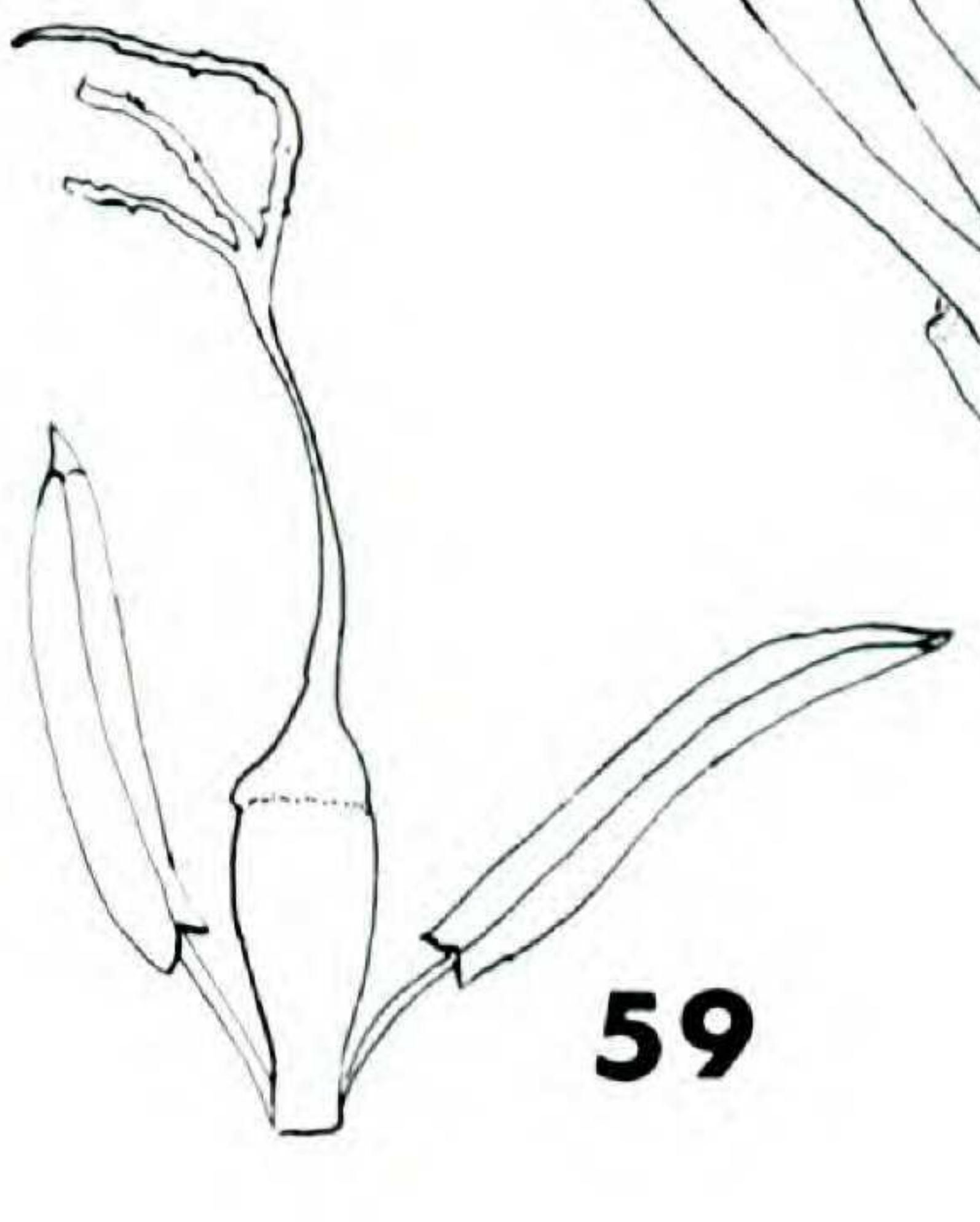

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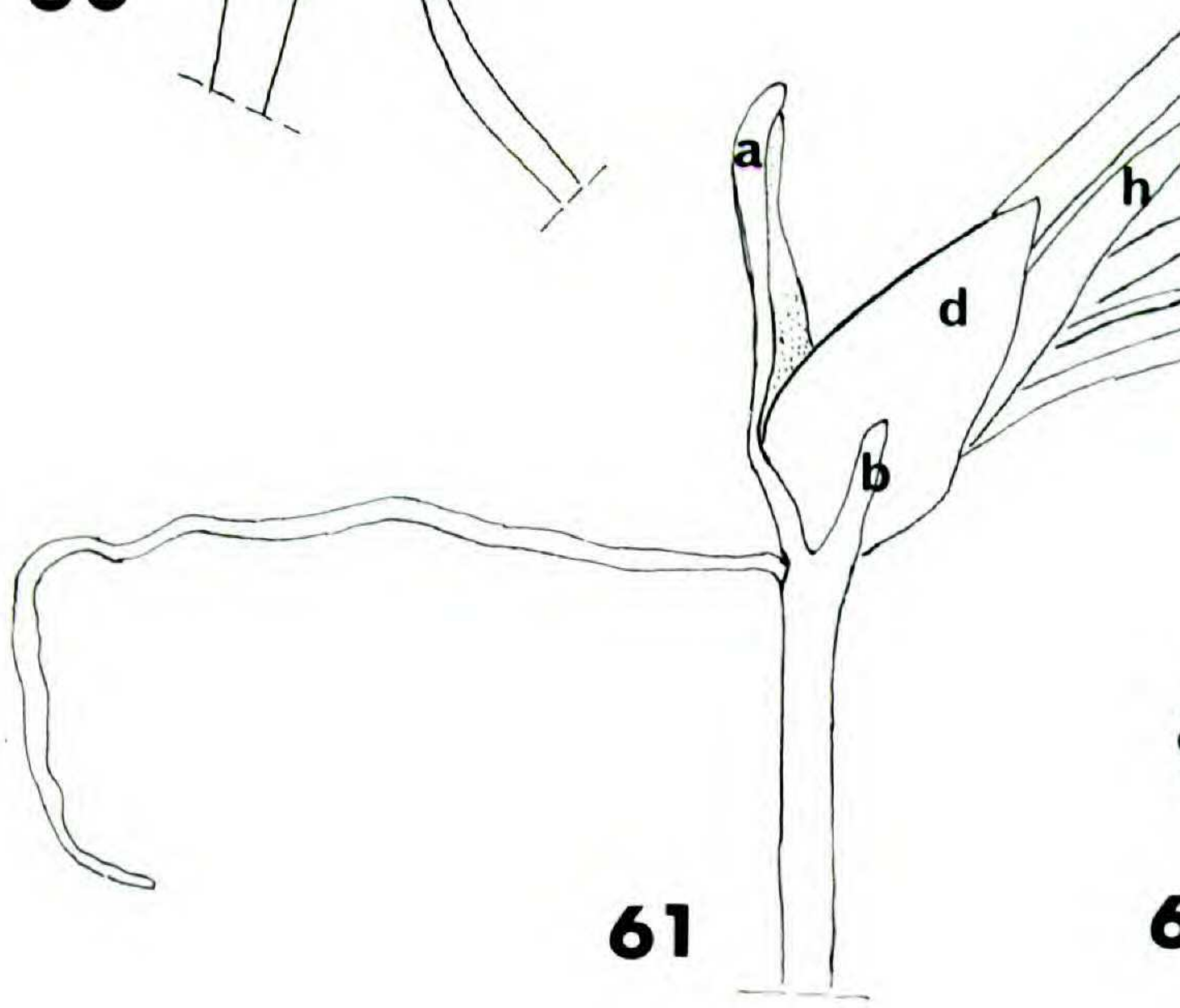

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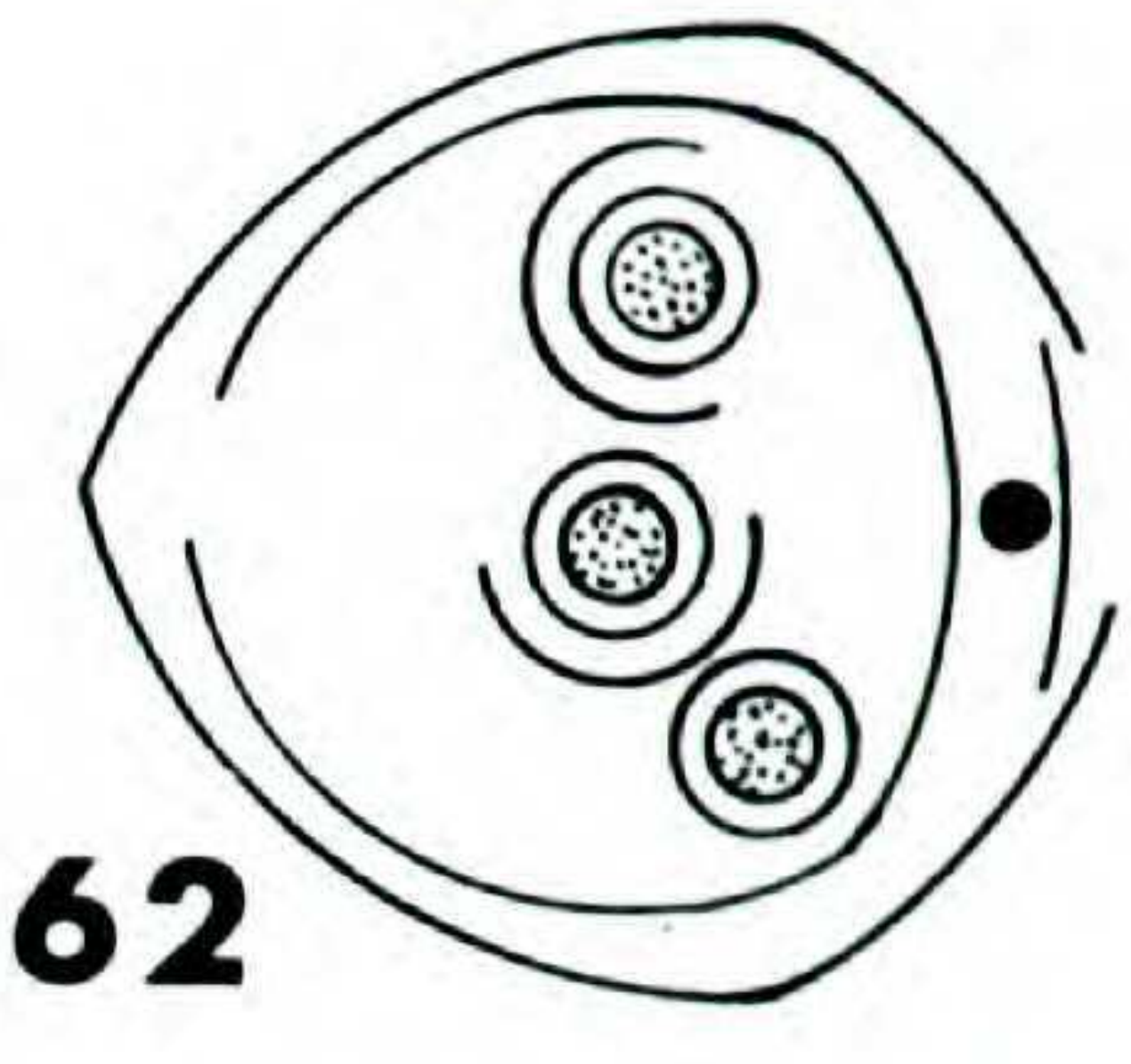

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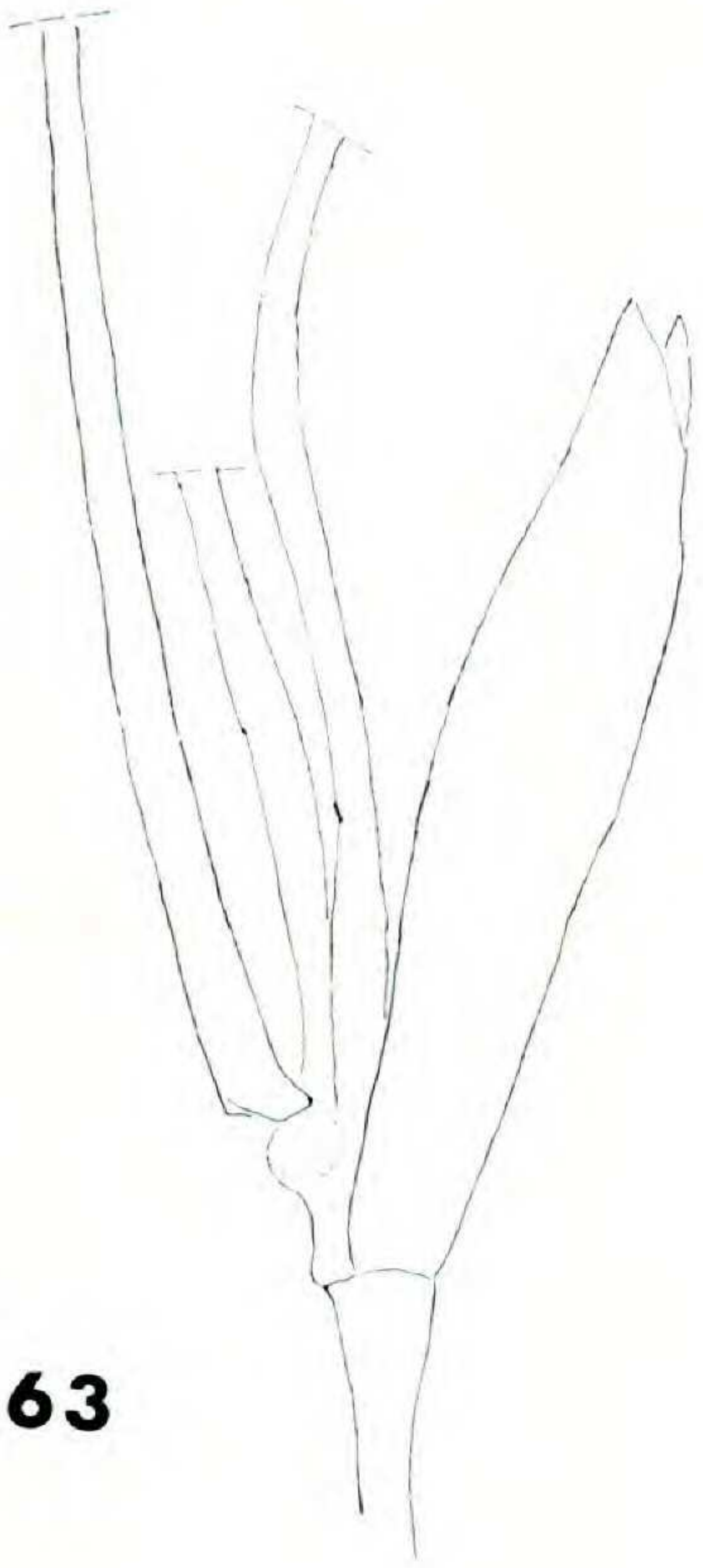

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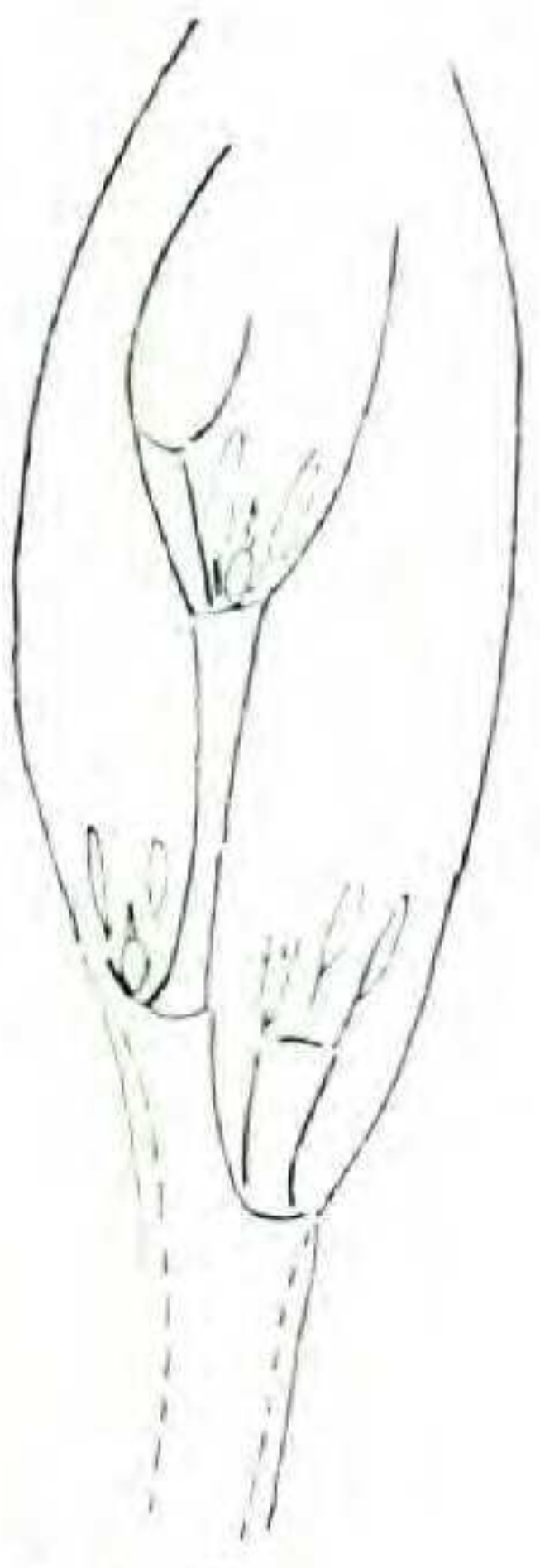

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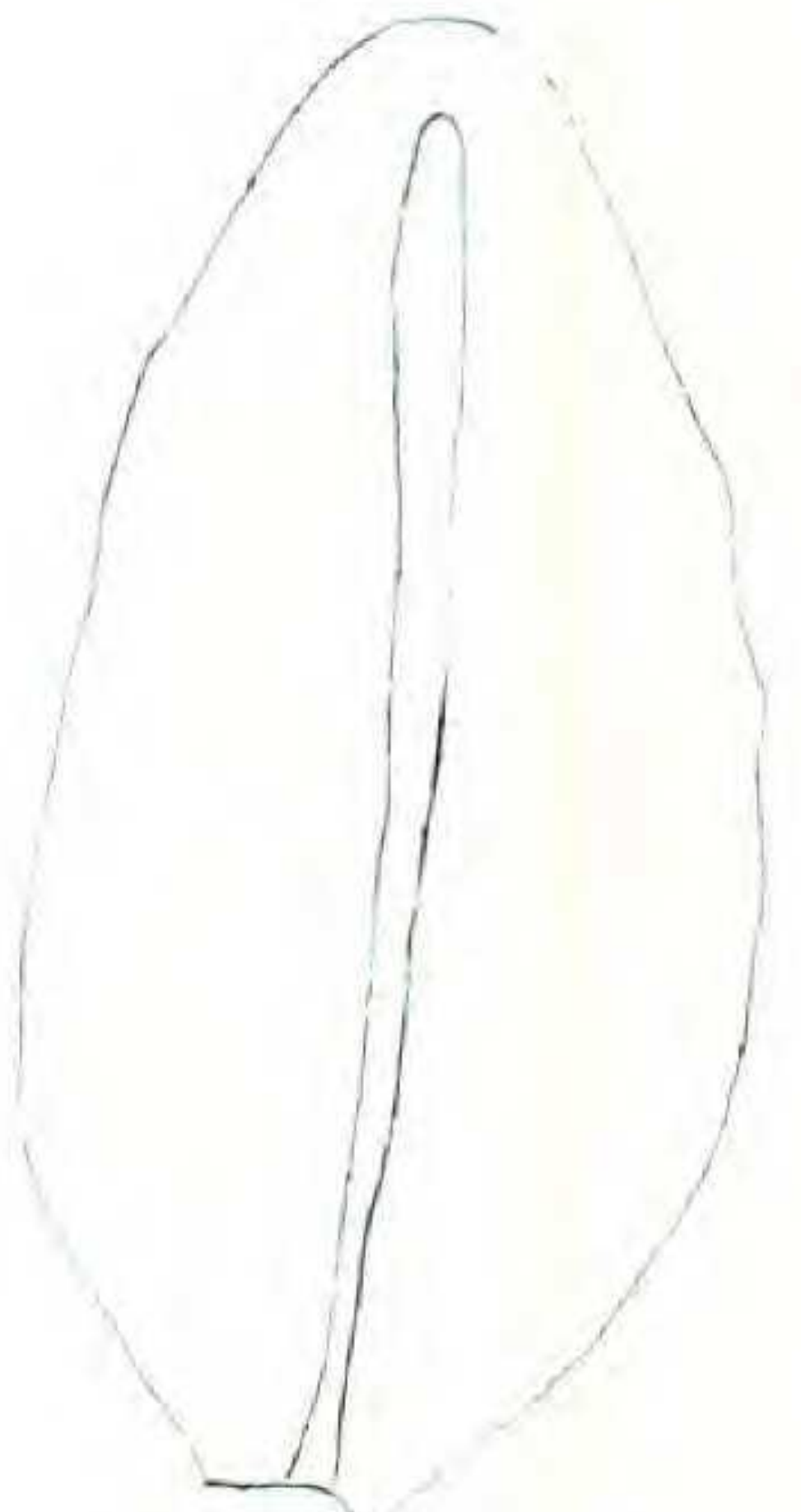

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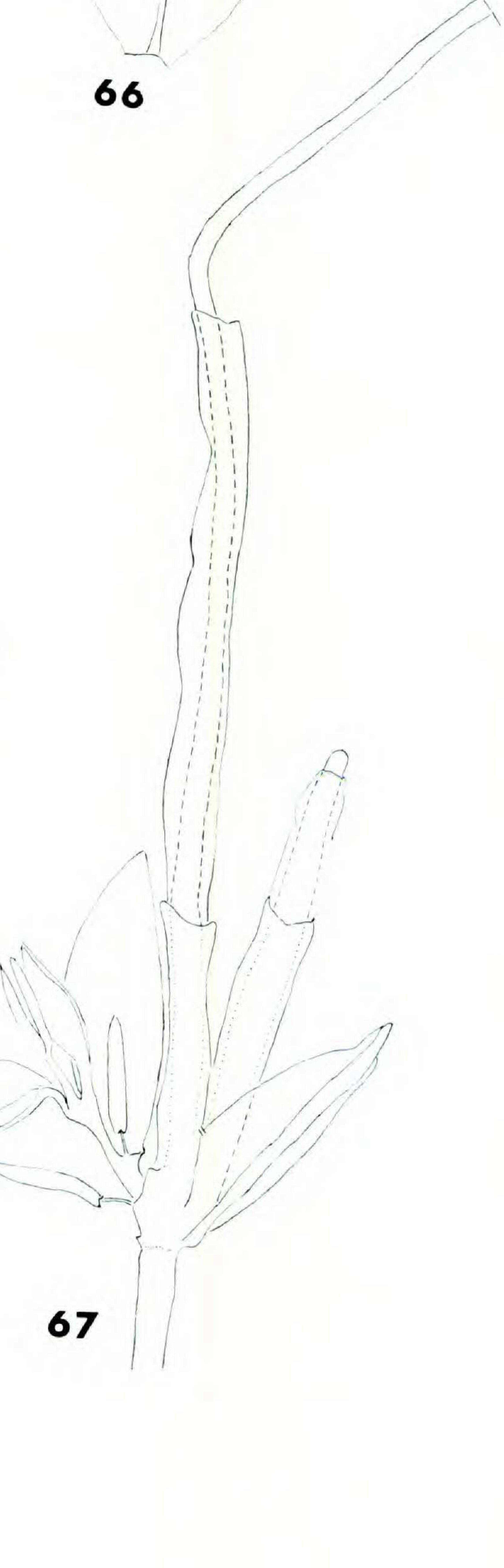

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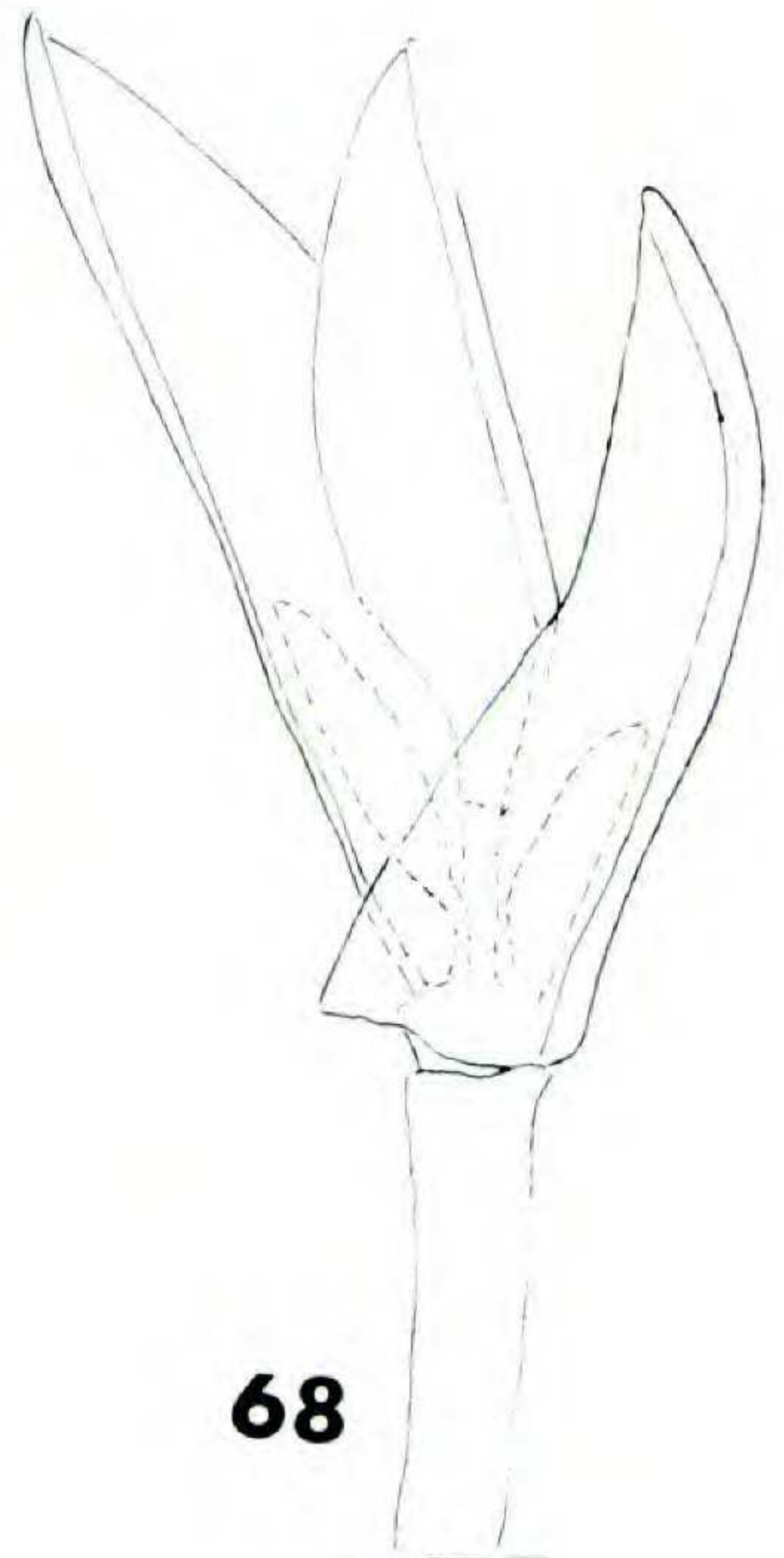

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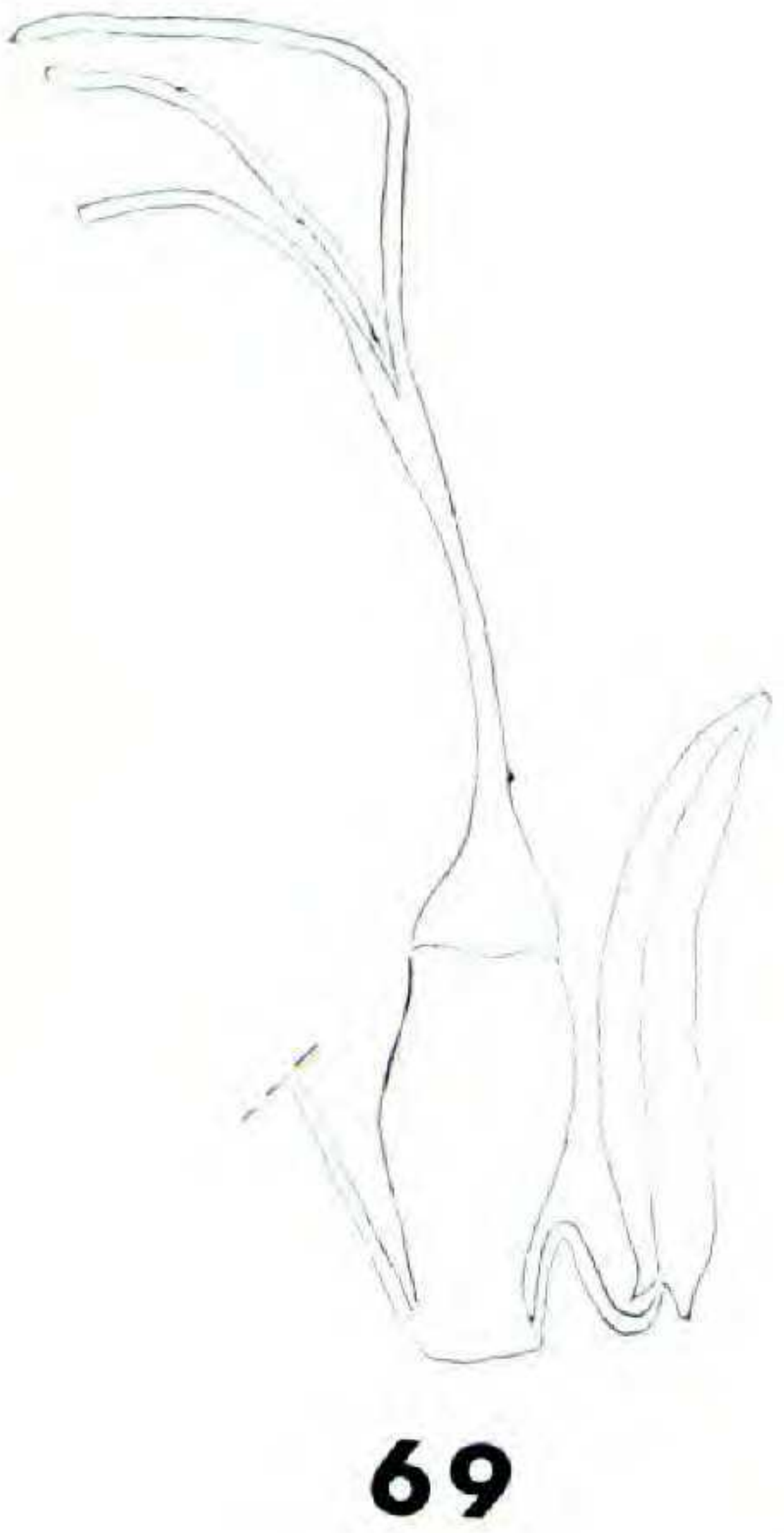

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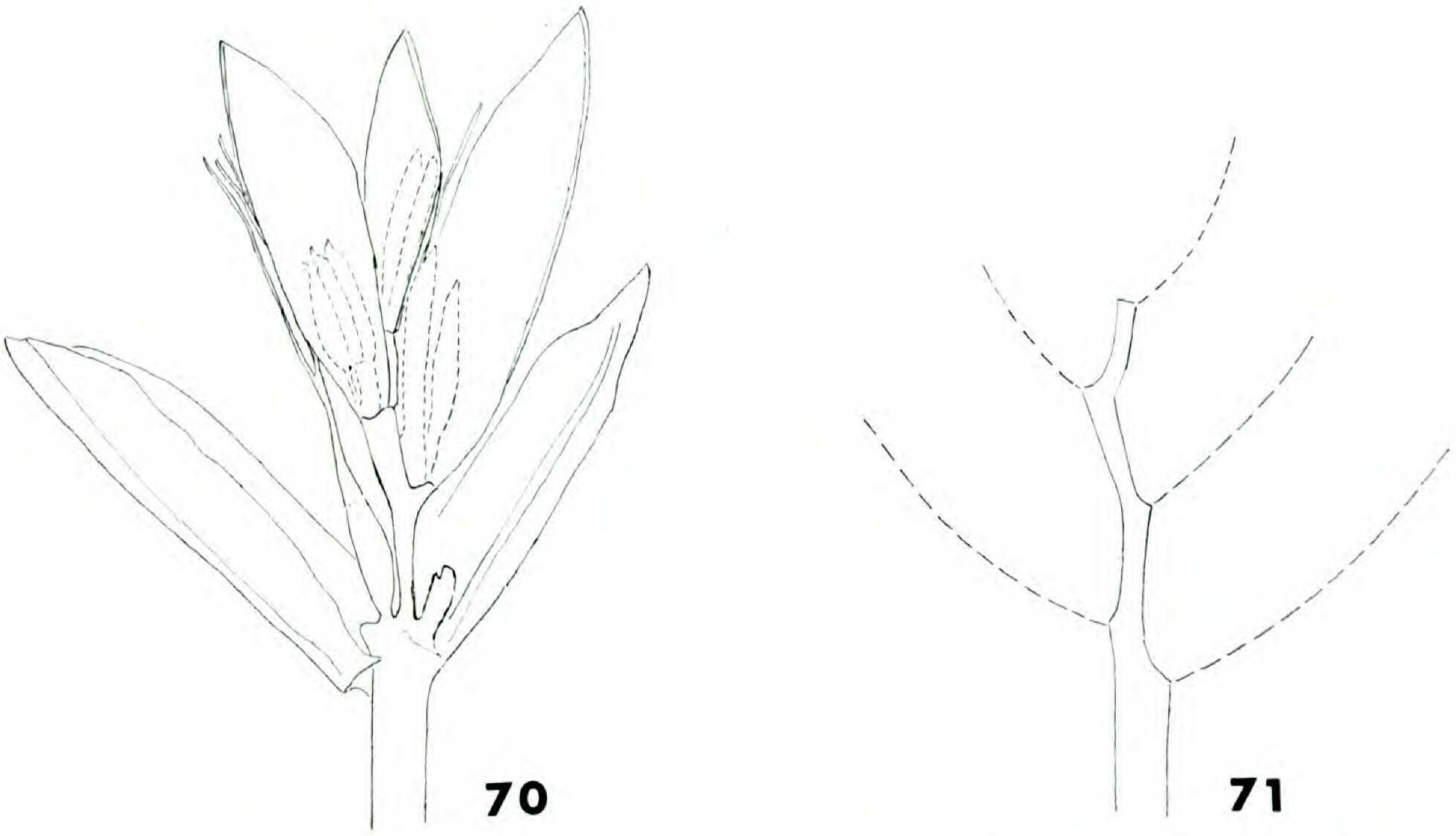


FIGURES 70–71.—70. Spikelet with four flowers; × 40. The associated scale shown at lower right has had its near side removed to show meristematic shoot rudiment in its axil. On left side is a detached first glume with a female flower in its axil. The three upper glumes have male flowers of 2–3 stamens each.—71. Diagram of spikelet of Fig. 70, showing form of rachilla and (in dashed lines) the position of associated scale and glumes. The interval between flower-bearing glumes usually decreases from base to apex, as here. Compare with Fig. 64, where the basal internode between flowering glumes is not the longest.

from my concept of the spikelet. As a consequence, I consider the rachilla only that part of the axis which starts at the node of the lowest true glume and continues distally. The rachilla bears the other laminar organs to which I prefer to restrict the term "glumes." The dimensions of the spikelets given here, however, include the associated scale when the axillary shoot is in the meristematic stage since this scale is then next to the glumes and difficult to exclude from the measurement; the dimensions given exclude the associated scale and the internode just above it when the shoot is well developed so that this scale is separated from the spikelet proper.

Not counting the associated scale, the spikelet in the type material has 3–5 delicate glumes disposed spirally or they are almost distichous. The associated scale, as stated, always has a meristematic or developed shoot in its axil; the glumes have flowers or are empty. The first true glume frequently has a bisexual or male flower, rarely a female flower, or is empty; sometimes the exact nature of the structure in the axil of this glume cannot be made out. The flowers in the second glume are bisexual or male, or rarely absent. The third glume may be empty, but usually has a male or bisexual flower. The fourth and fifth glumes usually are lacking, or when present are empty or the fourth has a male flower (Fig. 72). The rachilla is slightly zigzag (Figs. 64, 71).

The bisexual flowers have one pistil and 1–3 stamens; the male flowers have 1–2(–3) stamens. The ovary is obovoid-oblong, trigonous, topped by the conic

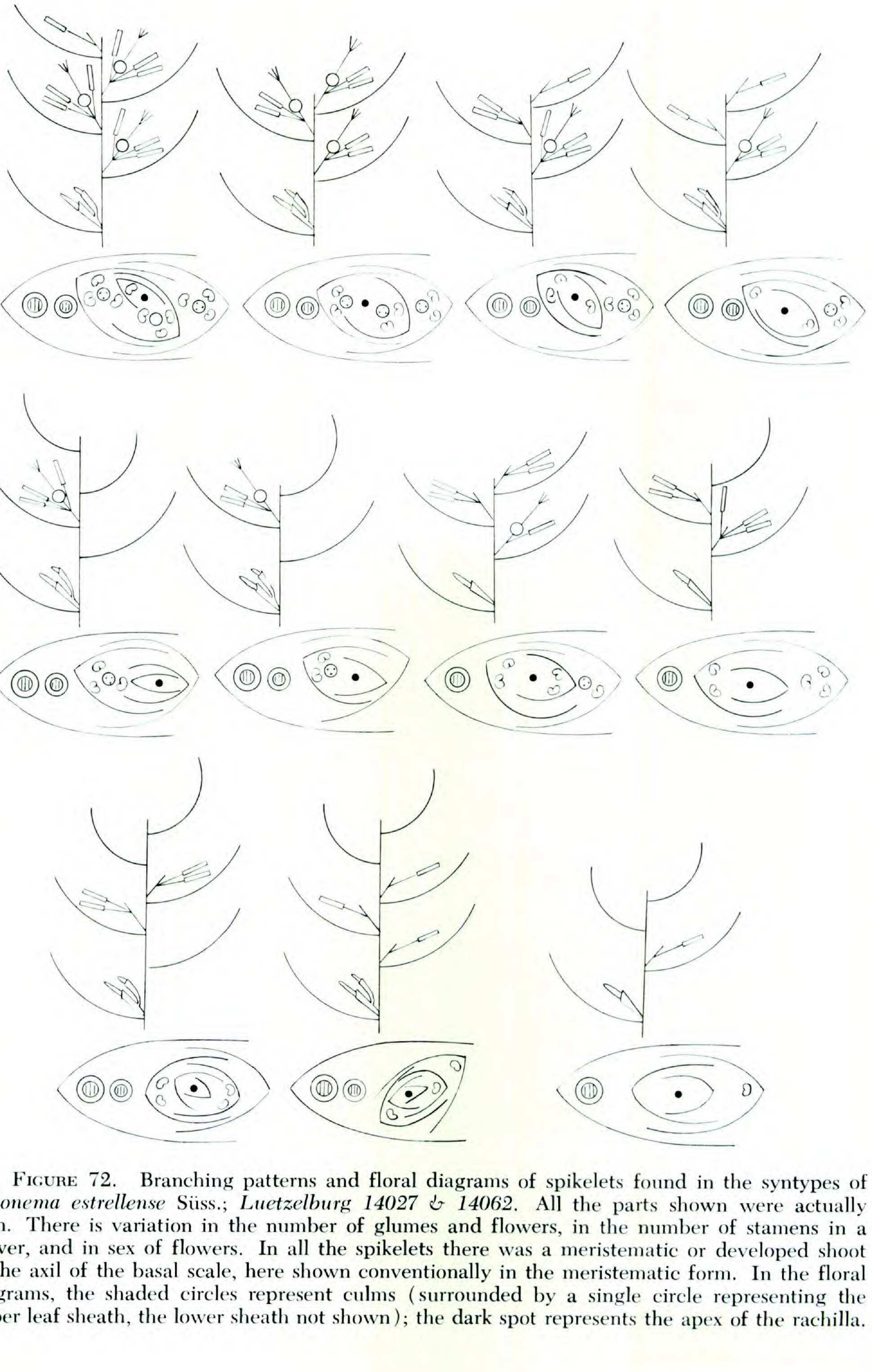
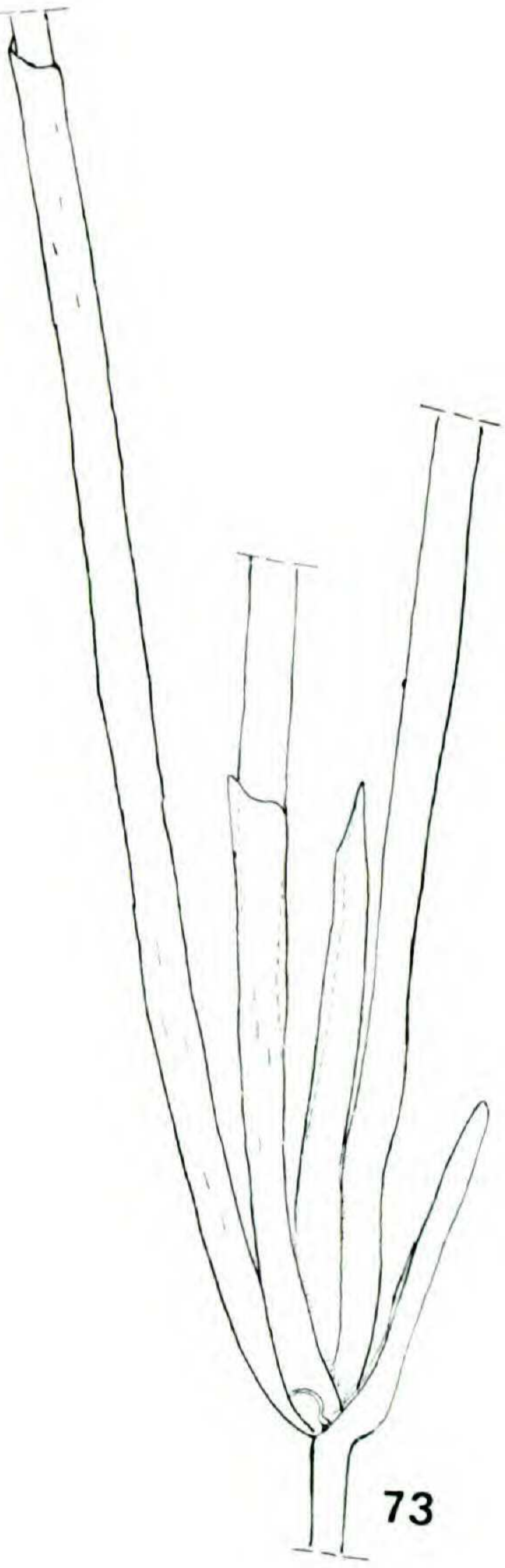


FIGURE 72. Branching patterns and floral diagrams of spikelets found in the syntypes of *Helonema estrellense* Süss.; *Luetzelburg 14027 & 14062*. All the parts shown were actually seen. There is variation in the number of glumes and flowers, in the number of stamens in a flower, and in sex of flowers. In all the spikelets there was a meristematic or developed shoot in the axil of the basal scale, here shown conventionally in the meristematic form. In the floral diagrams, the shaded circles represent culms (surrounded by a single circle representing the upper leaf sheath, the lower sheath not shown); the dark spot represents the apex of the rachilla.



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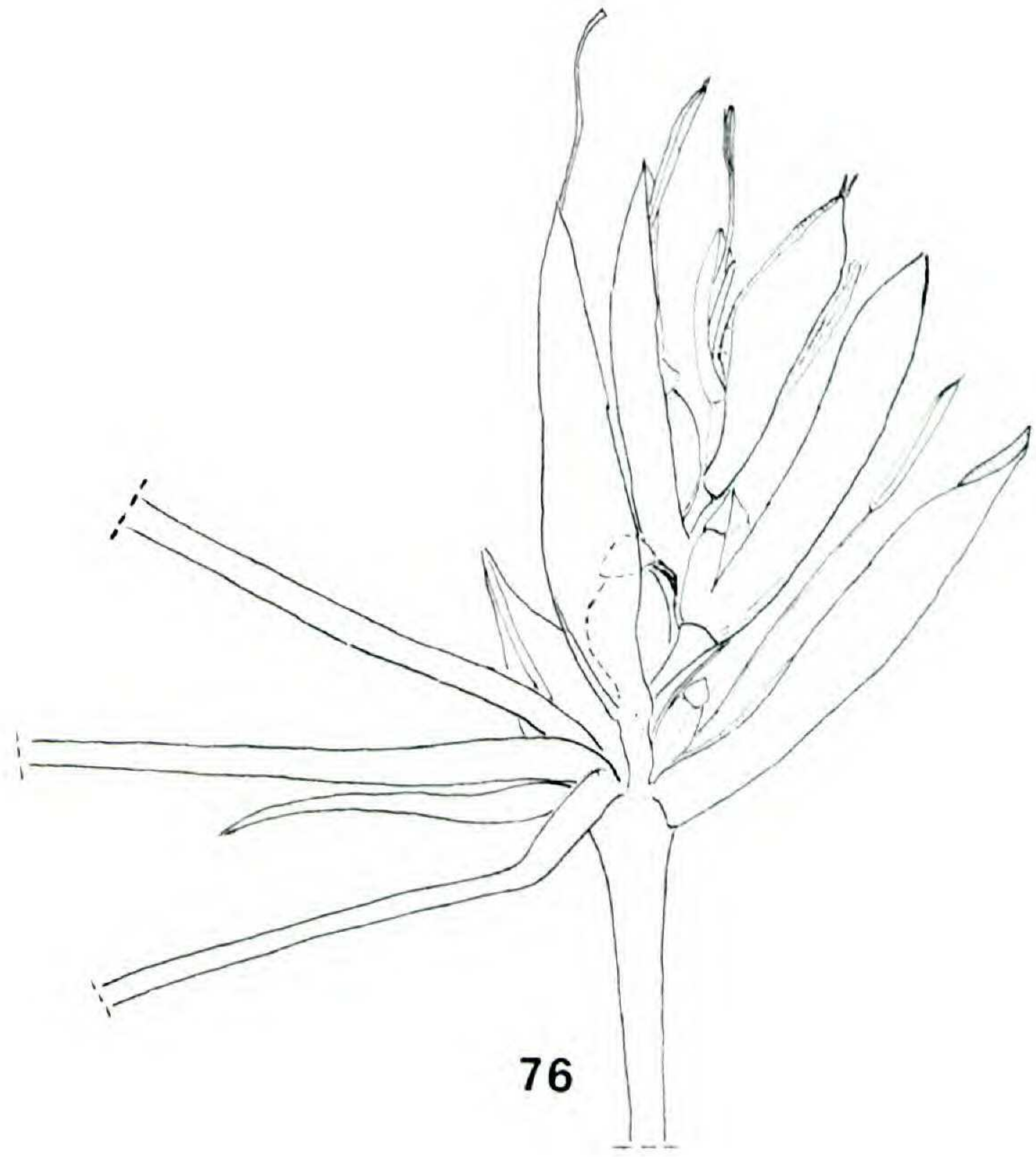

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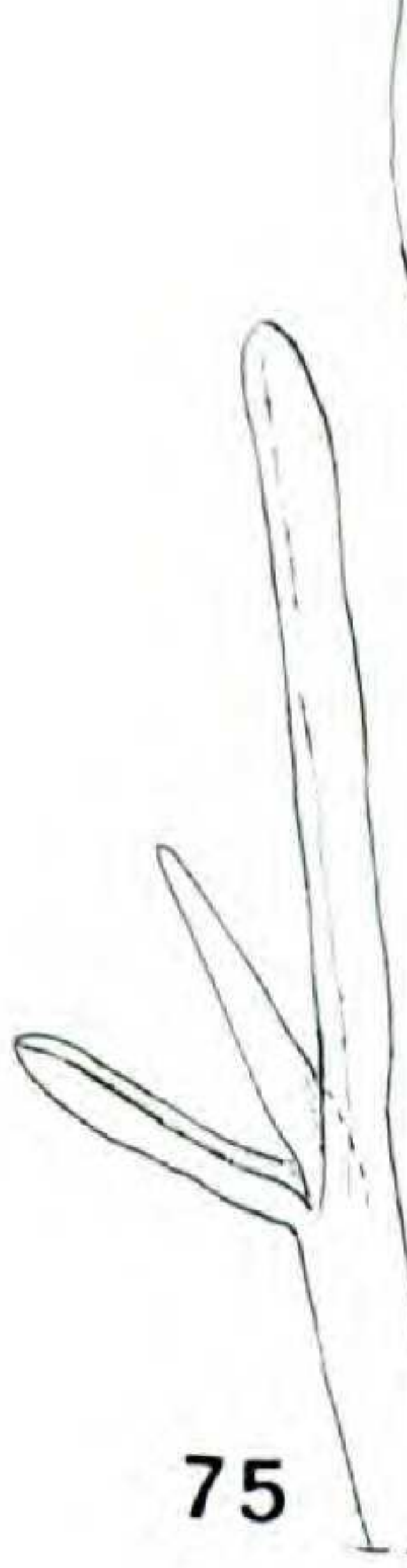

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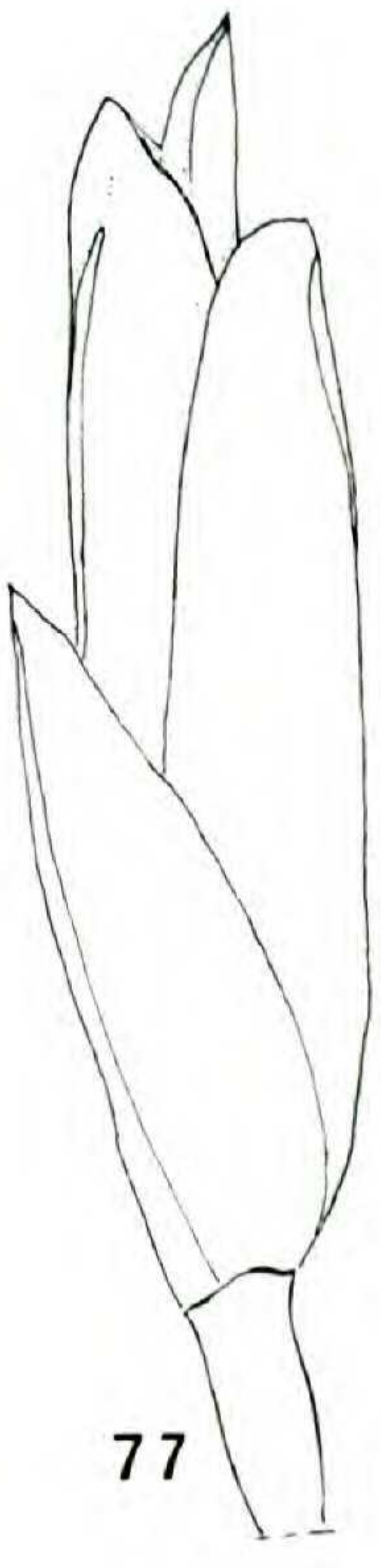

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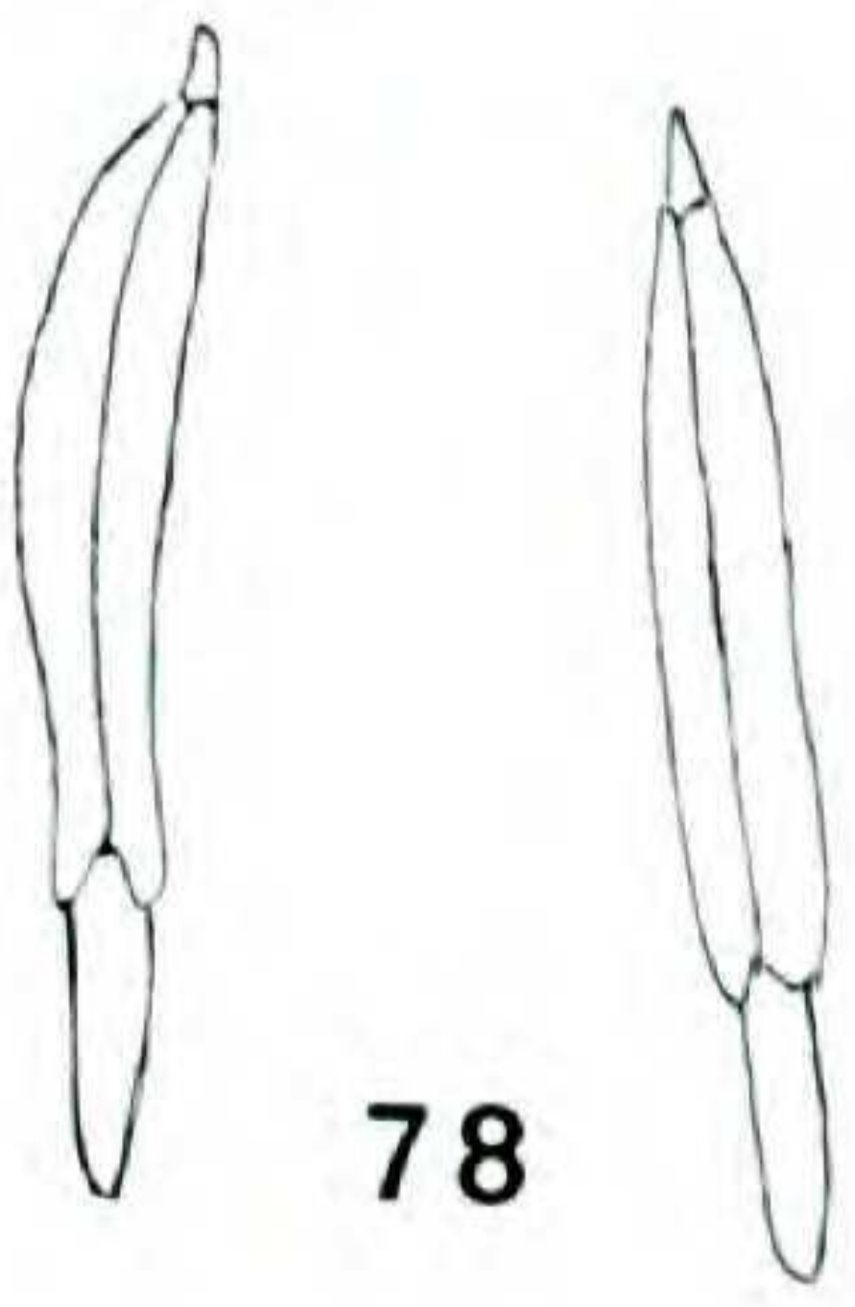

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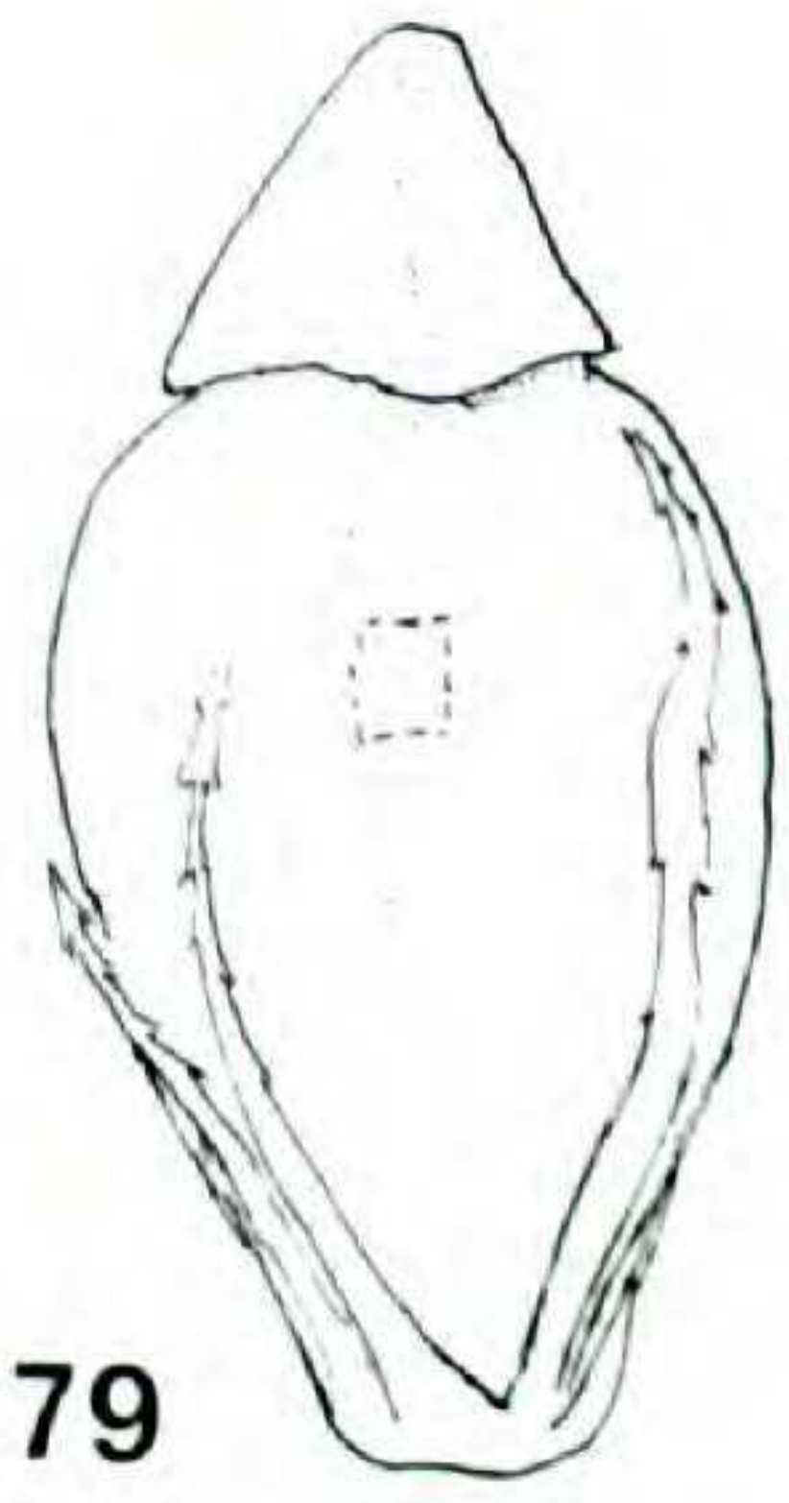

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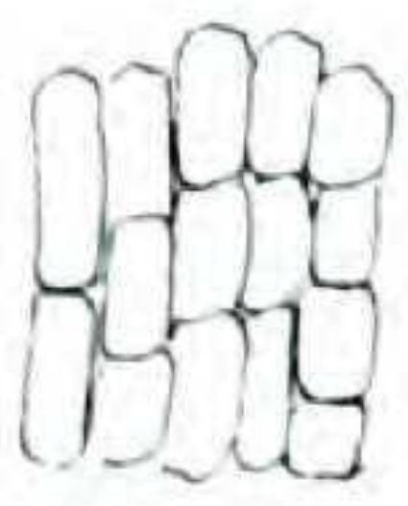

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stylebase which is slightly thickened and of a darker color than the body of the ovary. There are always three stigmatic branches. The anthers are apiculate and the base sagittate (Figs. 59, 69). Mature fruits and bristles were not found in the syntypes.

Süssenguth (1943) based his new genus *Helonema* on two Luetzelburg collections. I examined the sheets of these same collections and the above description was made from them. The spikelets were not much developed and contained male flowers as well as bisexual ones. But from the characters of the plant and its spikelet I early concluded that *Helonema* was really a species of *Eleocharis* (Eiten, 1961).

However, from this material only, the generic relationship could not be absolutely proven, nor whether the species was new or not. It was necessary to collect topotypes and cultivate them to obtain mature spikelets.

Living material was not found in the locality of one of the syntypes, which is a rock-bed stream in the canyon, "Grota do Inferno," cut into the steep seaward face of the Serra dos Órgãos just south of Teresópolis. It was found in the locality of the other syntype, in the small stream, Rio Gongoxoco (as it is now spelled), 2 km east of the railroad station and village of Saracuruna (previously called Rosário), near the main house of Fazenda Anhangá, in the Baixada do Rio de Janeiro, 26 km north of downtown Rio de Janeiro city. The "Baixada" is a flat marshy coastal plain lowland between the seacoast and the foot of the Serra dos Órgãos. The Rio Gongoxoco, therefore, is not in the Serra da Estrela (present spelling) as the label states. This serra starts a few kilometers north, being the steep seaward face of the Serra dos Órgãos leading up from the lowland to Petrópolis. The plant is aquatic and grows submersed rooted in the substrate or pieces float loose on the surface. The plants collected had exactly the same aspect as the type material but were completely sterile when found (Figs. 105–106).

Pieces from a single clone were cultivated submersed in an aquarium for two years and continued to grow in the same branched flaccid filamentous form but did not produce spikelets (Figs. 73–75). However, when ramets of the same

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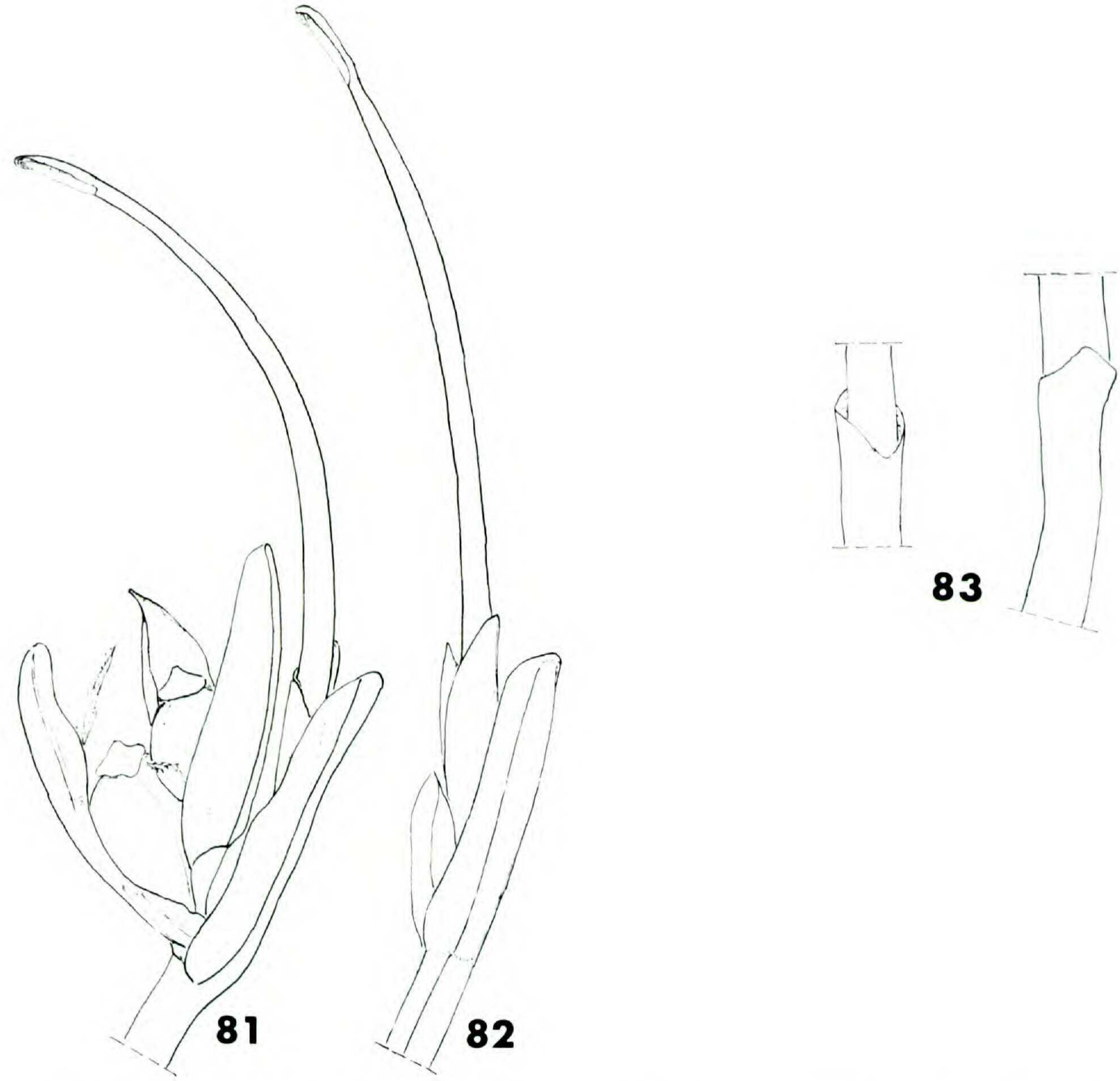
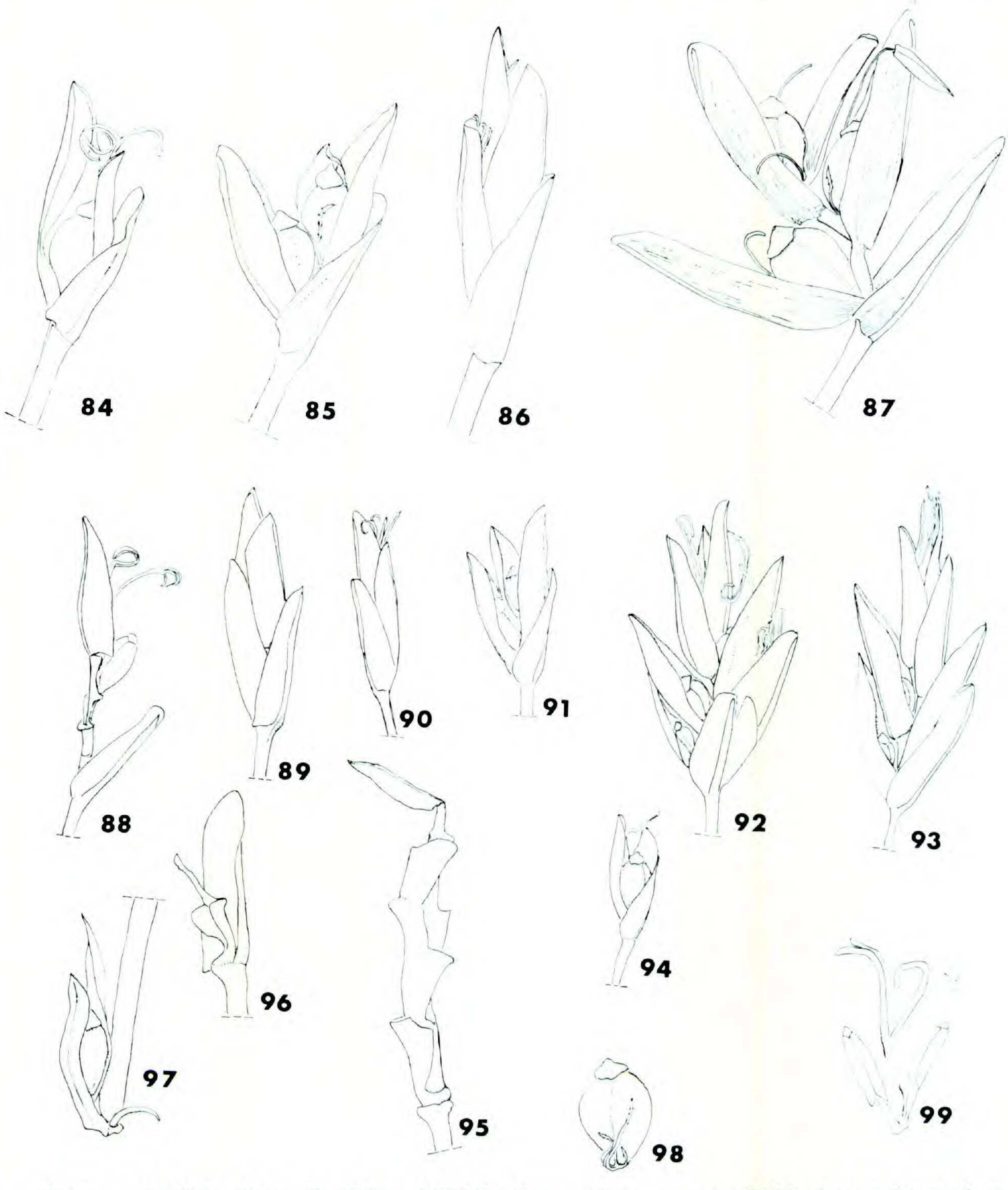
FIGURES 73–80. Topotype of *Helonema estrellense* Süss. (= *Eleocharis minima* Kunth). —73–75. *Eiten & Eiten 7242*. Plant cultivated in an aquarium under constant artificial light. The culm tips were 20 cm below the water surface.—73. Apex of culm with shoot; note lower external bract at base (upper bract and prophylls not seen), three developed culms, and a young culm still within its hood of leaf sheaths; × 16.—74. Tip of culm covered by bracts.—75. Same culm tip with the two bracts spread apart exposing meristematic culm tip; × 27. The plants shown in Figs. 76–108 are of this same clone grown under different conditions.—76–80. *Eiten & Eiten 8054-B*. Same clone as no. *7242*, but cultivated in a shallow, waterproof pot with forest soil covered with a few centimeters of water. The culm tips were 2 cm below the water surface when collected.—76. Culm tip with spikelet and associated shoot. The glumes have been spread apart to show fruits and flowers; × 16. The associated scale is behind the culms.—77. Spikelet without shoot; associated scale and glumes in natural position; × 16.—78. Young stamens with their filaments not yet elongated and anthers not yet shedding pollen; × 45.—79. Mature achene with bristles; × 40.—80. Detail of the square area in Fig. 79 showing the surface pattern of body of fruit; × 160.

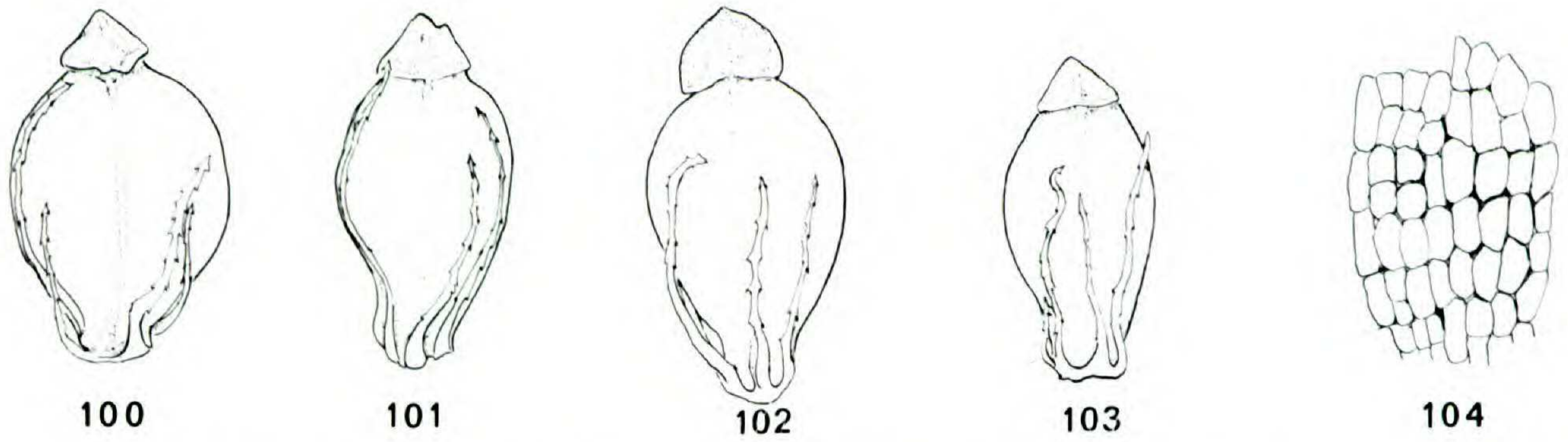


FIGURES 81–83. *Eiten & Eiten 8054-D*. Same clone as no. *7242* but cultivated in a pot with saturated forest soil, the shoots in air.—81. Culm-tip shoot of one culm with associated spikelet with mature achenes; × 28. Note culm growing from axil of associated scale (equivalent to lower external bract of shoot) and the lower achene in axil of upper bract here acting as lowest fertile glume.—82. Culm-tip shoot of one culm without associated spikelet; × 28. Note the two basal external bracts of the shoot (the lower subtending the new culm) and the two leaf sheaths with oblique mouths.—83. Two views of an inner leaf sheath, showing oblique mouth; × 28.

clone were planted in moist or saturated soil in pots, with the shoots growing in the air, the plants produced a completely different aspect: small tufts of thicker erect culms 2–22 cm tall (Figs. 107–108) with many well developed spikelets. The culms and their leaf sheaths (Fig. 83) were typical of *Eleocharis*, and almost all bore spikelets. Almost always, the spikelets were without associated shoots (Fig. 108: habit; Figs. 77, 86, 89, 90: spikelets in flower; Figs. 84–85, 87–88, 91–97, spikelets in ripe fruit or the fruits already fallen). In some of these cultures a very few of the culms did produce short culm-tip shoots, either without



FIGURES 84–99. *Eiten & Eiten 8054-C*. Same clone as no. *7242*, but cultivated in moist drained forest soil in pot.—84–87. Four spikelets (without associated culm-tip shoots) showing variation in number of glumes and fruits; × 19. In Figs. 84–86 the associated scale and glumes are in a natural position; in Fig. 87 they were spread apart. In the plants cultivated in this manner, the associated scale, besides bearing no flower, also does not have a meristematic rudimentary shoot in its axil.—88. Culm-tip spikelet; associated scale and uppermost glume remain, the other glumes have fallen; × 11.5.—89–90. Culm-tip spikelets in flower; × 11.5.—91–93. Culm-tip spikelets in fruit; × 11.5. The spreading apart of the glumes here is natural, caused by the growth of the achenes.—94. Culm-tip spikelet with associated scale and one glume. The single achene from the single lateral flower appears terminal on the rachilla apex; × 11.5.—95. Rachilla of a culm-tip spikelet from which the fruits, associated scale, and all glumes except the empty terminal one have fallen; × 19.—96. Rachilla of a culm-tip spikelet with associated scale still present and its achene and two glumes fallen; × 11.5.—97. Sessile spikelet on a very short axis, arising at base of clump among culm bases; × 11.5. Sessile spikelets are common in plants of this clone in this type of cultivation. Compare with *Eleocharis chamaegyne*.—98. Mature achene from culm-tip spikelet; × 19. Note bristles.—99. Young flower from culm-tip spikelet; × 19. In this stage bristles were not yet formed; they develop during the maturation of the fruits. Detail of stigmatic papillae on upper right.



FIGURES 100–104. *Eiten & Eiten 8054-C*. Mature achenes from same clone as no. *7242* but cultivated in moist drained soil in pot.—100–103. Achenes from different spikelets showing variation in form of body and stylebase; × 37. Note bristles.—104. Shallow-reticulate surface pattern of a mature fruit; × 93.5.

associated spikelets (Fig. 82) or with associated spikelets (Figs. 81, 107). All the flowers in the spikelets were bisexual with a pistil with three stigmatic branches and 2–3 stamens (Figs. 78, 99). Abundant mature achenes formed, always with bristles (Figs. 76, 79, 80–81, 84–85, 87–88, 91–94, 97–98, 100–104), but these bristles were not present in the young flower stage (Fig. 99). Meristematic vestiges of culm-tip shoots were absent in the axils of the associated scales (empty "lowest glume").

FIGURES 105–106. *Eiten & Eiten 7833*.—105. Recently collected plant that had grown submersed in its natural habitat in the Rio Gongoxoco photographed in a tray with water; × 0.5. (Collected in wild from same clump as no. *7242*.)—106. Single shoot; × 0.5. The plant floating in water in tray and its shadow make a double line.

Apparently, then, when the plant grows completely under water so that the culm tips are at least several centimeters under the surface, spikelets do not form, only well developed culm-tip shoots. When the plant is under water but the culm tips are near or at the surface (as in the case of the syntypes), small flowering spikelets (which probably do not go to seed) form on a few of the culm tips and developed or at least meristematic culm-tip shoots always form in the axil of the associated scale. When the plant or at least its culm tips is completely in the air, well developed, seed-bearing spikelets form which do not bear culm-tip shoots in the axil of the associated scale, not even in the meristematic form, or only bear such shoots extremely rarely. Water around the culm tip thus seems to discourage spikelet and seed formation and encourage vegetative shoot formation.

The habit and achenes of the topotype grown in and out of water prove that *Helonema* is really only an extreme submerged-aquatic ecological modification of a species of *Eleocharis*, *E. minima* Kunth. The plant fits perfectly the description of the species in Svenson's (1937) monograph.

Svenson (1937) states that in Brazil, *Eleocharis minima* has an aquatic phase, known as var. *ambigua* (Steud.) Kük. The drawing he gives for this variety (his Plate 462, Fig. 4) shows a tufted plant with erect stems with spikelets; from the base of two of the spikelets a few roots grow out. This habit is almost identical to the typical terrestrial habit of the species; it is definitely not the habit of *Helonema*. Since ramets of the same clone develop the *Helonema* habit when grown submersed and the typical *E. minima* habit when grown emersed, the *Helonema* habit is not a genetic form and should not have a formal taxonomic name. Since the variety *ambigua* is even less different from the typical form and is also very unlikely to be a genetically fixed form, it should not be maintained as a variety.

Other collections of *Eleocharis minima* studied (det. L. T. Eiten):

Eleocharis minima Kunth var. *minima* (topotypes of *Helonema estrellense* Süss., all in herb SP. Duplicates of the following collections will be distributed to other herbaria.)

BRAZIL. RIO DE JANEIRO: Mun. de Duque de Caxias, Fazenda Anhangá, 22°40'S. 43°14'W., Rio Gongoxoco, 100–200 m from its mouth in the Rio Imbariê, plant submersed in clear water near bank, 25 Apr. 1966, *Eiten & Eiten 7225, 7228, 7233, 7234, 7235*. Same place, plant rooted in substrate, submersed in 0.5 m of clear water, 25 Apr. 1966, *Eiten & Eiten 7226*. Same place, mouth of Rio Gongoxoco where it empties into Rio Imbariê, plant growing fixed to concrete wall of small dam, submersed under 2 dm of clear water, 25 Apr. 1966, *Eiten & Eiten 7240*. Same place, plant growing as large cushion over drainage pipe, submersed in 3 dm of clear water, 25 Apr. 1966, *Eiten & Eiten 7241, 7242, 7243*. Same place, plant growing as a cushion over drainage pipe, submersed in 6 dm of clear water (from same clump as no. 7242), 20 Nov. 1966, *Eiten & Eiten 7833*. Mun. de Itaguá, Instituto de Pesquisa e Experimentação Agrícola do Centro-Sul, topotype material of *Eiten 7242* cultivated in continually saturated soil, 19 Nov. 1966, *Eiten & Eiten 7800*. Same place, same topotype material, cultivated in continually saturated soil, 21 Nov. 1966, *Eiten & Eiten 7878*. SÃO PAULO: Mun. de São Paulo, city of São Paulo, Parque do Estado, Instituto de Botânica, same topotype material (*Eiten 7242*) cultivated submersed in 25 cm of water, tips of culms floating on surface, Mar.–Apr. 1967, *Eiten & Eiten 8054-B*. Same place, same topotype material, cultivated emersed in pot, rooted in moist drained soil, Jan.–Feb. 1967, *Eiten & Eiten 8054-C*. Same place, same topotype material, cultivated emersed in pot, rooted in saturated soil, Mar.–Apr. 1967, *Eiten & Eiten 8054-D*.

Eleocharis minima Kunth var. *minima* (aquatic habit like that of *Helonema*).

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FIGURES 107–108. Cultivated topotypes.—107. *Eiten & Eiten 7878.* Same clone as no. *7242* but cultivated emersed in continually saturated soil in the Baixada do Rio de Janeiro; × 0.3.—108. *Eiten & Eiten 8054-D.* Same clone as no. *7242* but cultivated emersed in continually saturated soil in São Paulo city; × 0.5.

UNITED STATES. FLORIDA: Seminole Co., Lake Adelaide, on bottom and floating, 10 Sep. 1955, *Schallert 24132* (UB).

BRAZIL. PARÁ: Rio Itacaiuna, Seco-Grande, 20 June 1949, *Fróes & Black 24608* (UB).

Eleocharis minima Kunth var. *minima* (terrestrial habit).

BRAZIL. PARÁ: Almeirim, campo inundado do Jutahy, flutua na água, 14 Apr. 1923, *Ducke s.n.* (RB). MARANHÃO: perto de Carolina, [wet place in region of] campo cerrado, 26 May 1950, *Pires & Black 2179* (IAN). MATO GROSSO: Corumbá, parte alagável da margem do [Rio] Paraguay, 20 Oct. 1953, *Pereira et al. 164* (RB). BAHIA: *Bondar 37162* (SP). This collection has basal spikelets with mature fruits. RIO DE JANEIRO: Petrópolis, Caetitu, brejo, Mar. 1944, *Góes & Constantino 289* (RB). SÃO PAULO: Mun. de São Paulo, city of São Paulo, Barra Funda, July 1885, *Loefgren 9186* (SP). Mun. de Mogi-Mirim, aquática submersa, 25 May 1927, *Hoehne 20513* (SP). Mun. de Mogi-Guaçu, Fazenda Campininha, brookside, saturated

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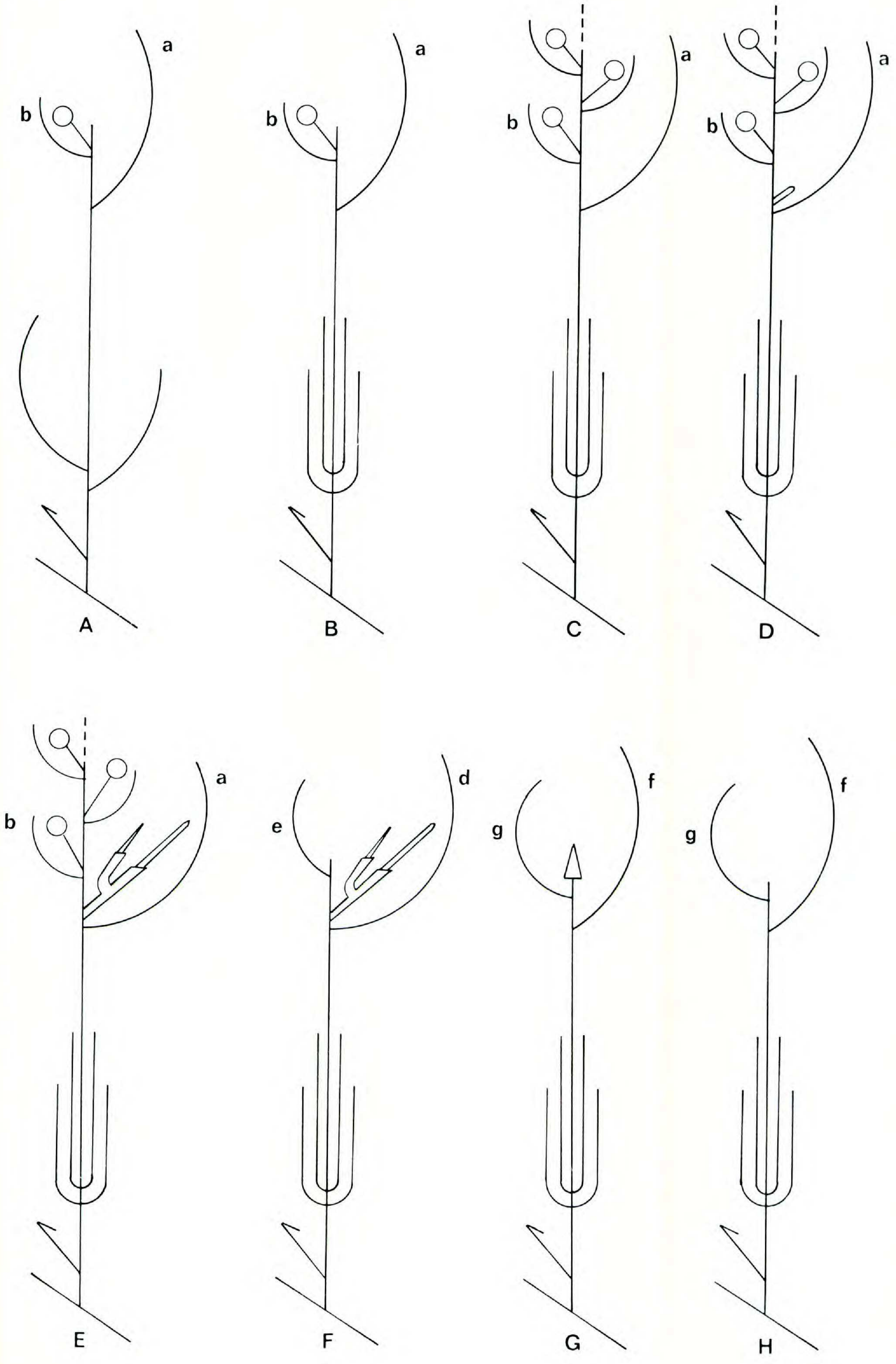
FIGURE 109. Structure of culm and its appendages in *Eleocharis* and its derived genera, *Websteria* and *Egleria.*—A. Short axis of *E. chamaegyne.*—B. Long axis (culm) of *E. chamaegyne* and other *Eleocharis* spp. with 1-flowered spikelets and of *Websteria.*—C. *Eleocharis* spp. with many-flowered spikelets and *Egleria.*—D. Culm with spikelet and vestigial vegetative shoot in axil of associated scale in syntypes of *Helonema* (*E. minima*).—E. *Eleocharis* spp. with spikelet and associated culm-tip shoot.—F. *Eleocharis* spp. and *Websteria* with culm-tip shoot without associated spikelet.—G. *Eleocharis* spp. with vestigial spikelet (such as *E. interstincta*).—H. *Eleocharis* spp. culm whose tip bears neither shoot nor spikelet. Note homology of associated scale, a, to lower external bract at base of a culm-tip shoot, d, and to lower bract of a culm tip without shoot or spikelet, f; and homology of lowest true glume of a spikelet, b, to upper external bract at the base of a culm-tip shoot, e, and to upper bract of a culm tip without shoot or spikelet, g.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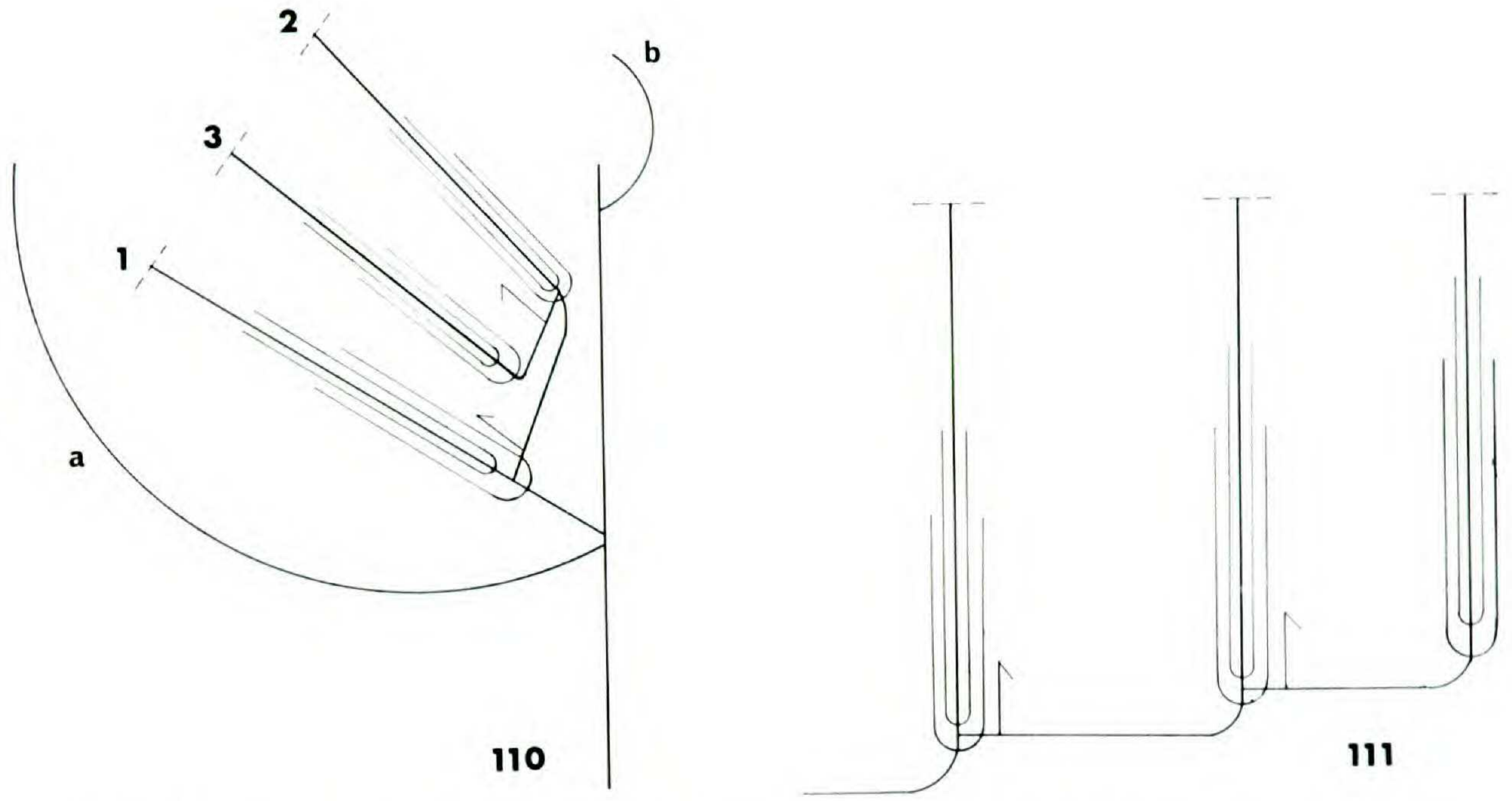


FIGURES 110–111.—110. Branching pattern and relation of leaf sheaths and prophylls in a culm-tip shoot of *Eleocharis* and *Websteria*. Three culms (numbered in the order of their appearance) are shown in this shoot. Note that the first culm, although a branch, does not bear a prophyll but the other culms do. The new culms are shown here arising in the axil of the lower leaf sheath but in some species they appear to arise in the axil of the upper leaf sheath. Note that the prophyll on the axis of culm 2 (addorsed to culm 1) has become separated from the leaf sheaths of its culm by the growth of culm 3. a = lower external bract at base of shoot; b = upper external bract at base of shoot.—111. Branching pattern of rhizome and culms in *Eleocharis*. The prophyll of a culm axis is at some distance from the leaf sheaths of that axis when the rhizome internodes are long. Note that the rhizome is sympodial, made up of the first two basal internodes of each succeeding branch. The first of these two basal internodes is the short subprophyllar internode (between the origin of the axis and the prophyll node); the second is the longer internode between the prophyll node and the node of the lower leaf sheath on the upturned part of the axis that forms the culm. When older, more culms may arise at a rhizome node, the branching being the same as that shown in Fig. 110. The bases of all the culms at one rhizome node then thicken and become concrescent, forming a corm, which is the solid center of a tuft of culms.

soil, 22 Apr. 1960, *Eiten & Eiten 1986* (SP, UB). Same place and habitat, 23 Sep. 1960, *Eiten & Eiten 2397-A* (SP).

PARAGUAY: Near Puerto Casado, 22 Oct. 1893, *Lindman 2295* (R). Cited in Svenson's monograph (1937).

Eleocharis minima Kunth var. *bicolor* (Chapman) Svenson (terrestrial habit).

BRAZIL. SÃO PAULO: Mun. de Mogi-Guaçu, Fazenda Campininha, brookside, saturated soil, 3 Sep. 1960, *Eiten & Eiten 2301-A* (SP).

Figure 109 gives diagrams of the structure of culms and spikelets in *Eleocharis* and the related genera *Websteria* and *Egleria* (Eiten, 1964) to illustrate the terminology used in this paper. The figure shows several homologies: (1) between the lower, usually two short scales on the short axis of *E. chamaegyne* and the usual two leaf sheaths in the genus; (2) between the associated scale at the base of the spikelet and the lower of the two external bracts at the base of a culm-tip shoot, and between them and the lower of the two scalelike bracts that covers a culm tip without shoot or spikelet; (3) between the lowest true glume of a spikelet (that which bears the lowest flower) and the upper external bract at the base of a culm-tip shoot, and between them and the upper scalelike bract of a culm tip without shoot or spikelet. The prophyll is shown in Fig. 109 next to the leaf sheaths of its own axis, but when the next culm of the shoot develops, this will often grow between this prophyll and the leaf sheaths, thus separating them. The third culm to develop (from the base of the second culm) will separate the first prophyll and the leaf sheaths of its axis even more, etc. (Fig. 110). Only the first culm in a culm-tip shoot does not bear a prophyll. A prophyll will also be separated from the leaf sheaths of its axis when the culm is the upturned end of an axis whose lower two internodes form part of a rhizome (Fig. 111).

Figure 109 shows that the lamina called the associated scale never bears a flower and for this reason I prefer not to call it a glume. It may be empty or bear a vestigial or developed culm in its axil, which in turn may bear a culm at its base in the axil of a leaf sheath, and this another culm, etc., so forming a shoot (Fig. 110). This is not a case of vivipary in the strict sense for the shoot does not arise from a seed germinating while still on the plant; neither is it a case of vivipary in a looser sense, for the shoot never grows from the axil of a true flower-bearing glume. It grows out only from this one location, which never does bear a flower. The associated scale in *Eleocharis* and its derived genera seems to be of a different nature from the empty, non-prophyll, lower glumes in other genera such as *Rhynchospora*, *Cladium*, etc., which never bear vegetative shoots in their axils and which can be considered to be flower-bearing true glumes that have become sterile.

BISBOECKELERA PAPORIENSIS Süss.

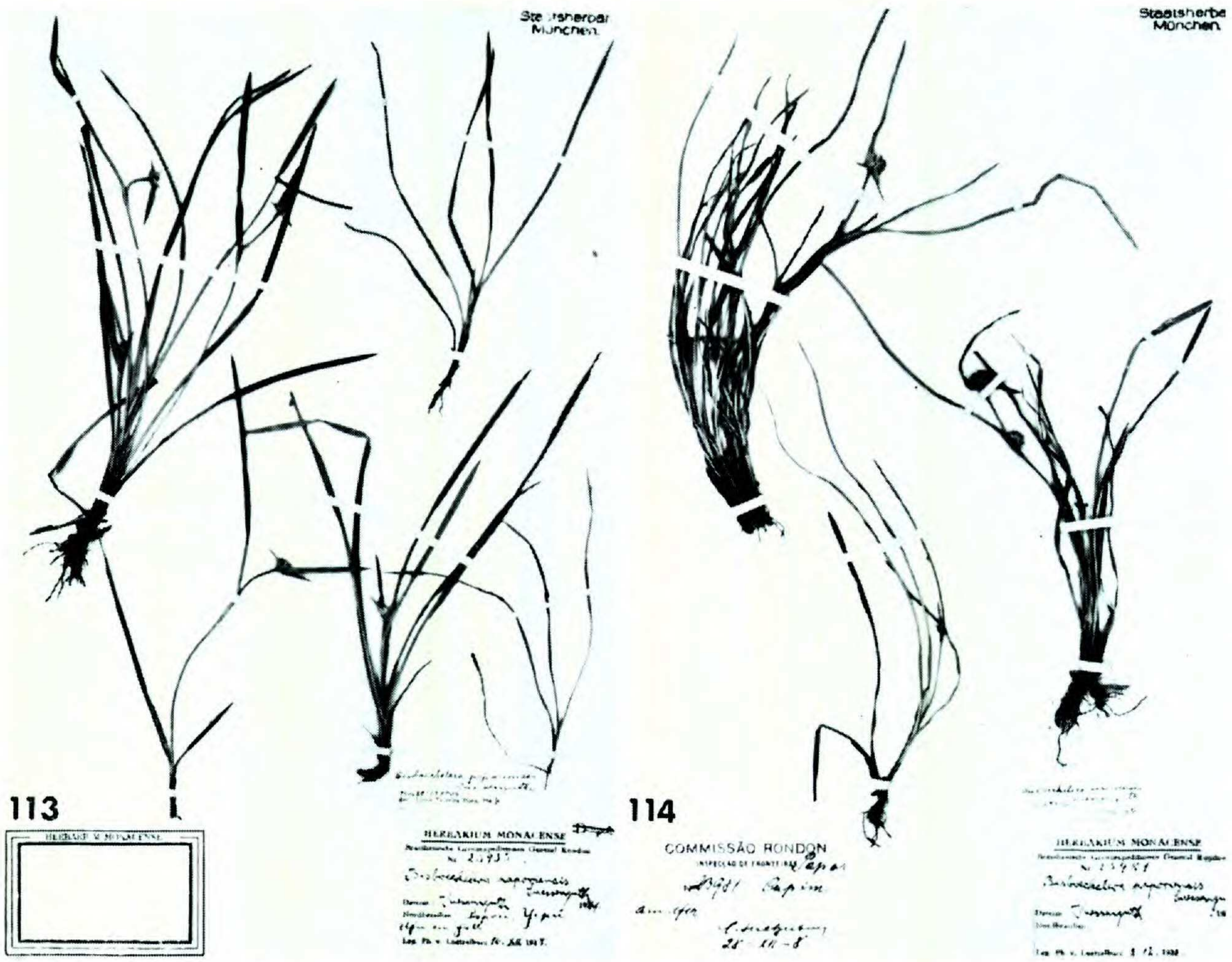
(= *Diplacrum longifolium* (Griseb.) Clarke)

Description of syntypes of *Bisboeckelera paporiensis* Süss., Bot. Jahrb. Syst. 73: 120–121. 1943: Grenze Brasilien-Kolumbien, Gebiet des Rio Papori, Yapú, Ufer am Fall, 16 Dec. 1928, *Luetzelburg 23955* (M). Ebenda Capim am Ufer, 8 Dec. 1928, *Luetzelburg 23981* (M).

The plant is 20–35 cm tall with culms 5–20 cm long, triangular in cross section with concave faces and salient veins (Figs. 112–115). Each culm has 2–3 basal leaves 15–22 cm long and 2.7–3.5 mm wide; the leaves are flat, linear, with visible small teeth on the margins near the apex, and have 15 veins, of which two lateral ones are evident and denticulate near the apex. The sheath is 2.0–3.0 cm long, purplish-red, the contralaminar side (the side opposite to the side which bears the blade) membranous and the mouth with a triangular appendage 1.5 mm long.

The inflorescence is made up of 1–2 heads (capitula) 5–12 mm wide and 5–7 mm tall; when there are two heads in an inflorescence the lower is always smaller. There is one cauline leaf 8.5–19.5 cm long and 2.5–3.5 mm wide. On culms with two heads, this leaf subtends the lower head (Fig. 115). Three visible bracts are associated with the upper head; these in order have the following lengths: 2–6 cm, 1–3.5 cm, and 0.8–1.7 cm. The other bracts, inside the heads, are very small and not evident. The peduncles of the heads are 0.8–8.5 cm long.

FIGURE 112. Lectotype sheet of *Bisboeckelera paporiensis* Süss. (= *Diplacrum longifolium* (Griseb.) Clarke); *Luetzelburg 23955*; × 0.4. Figures 116–118, 131–153 were made from plants of this collection.



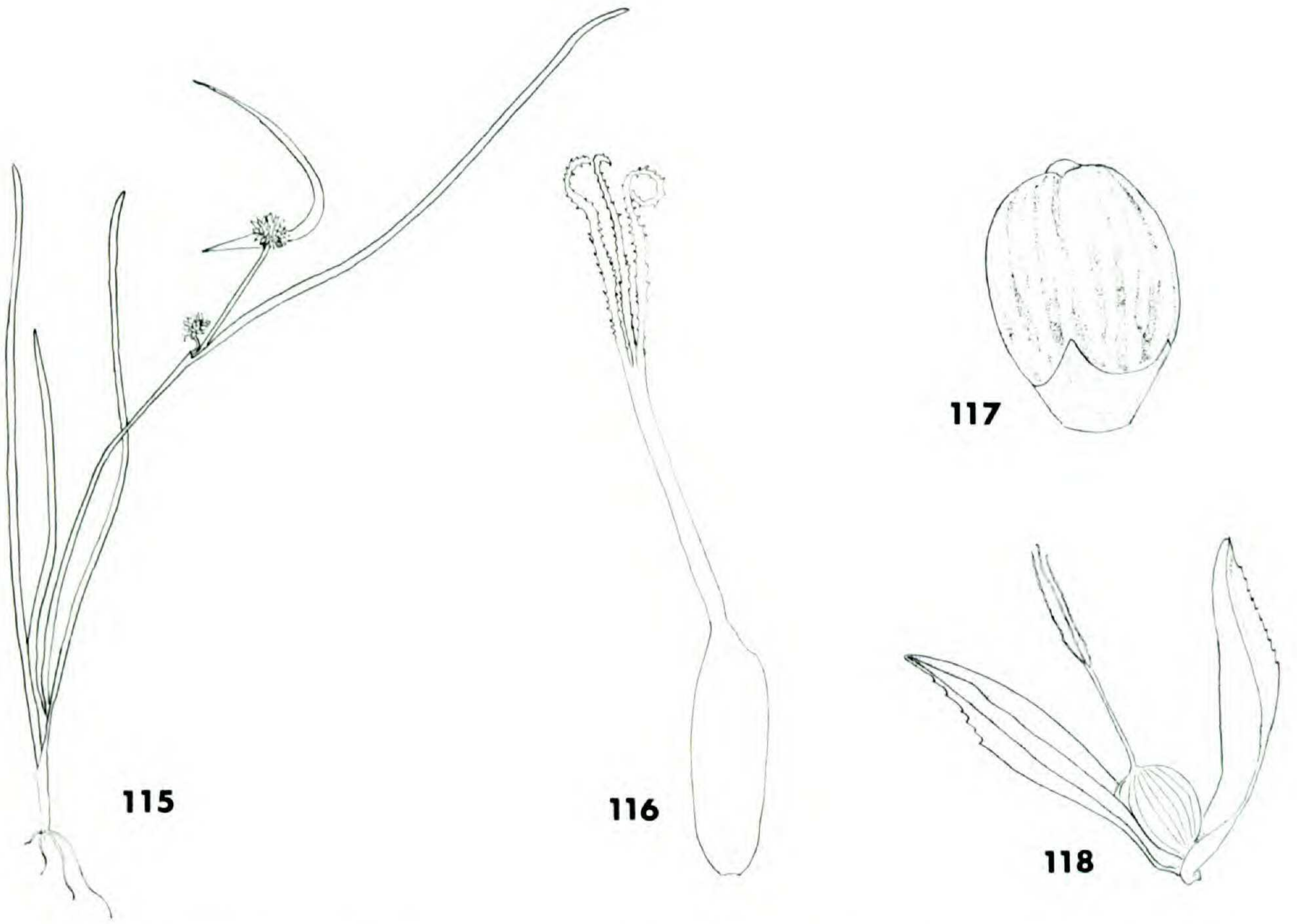
FIGURES 113–114. *Bisboeckelera paporiensis* Süss. (= *Diplacrum longifolium* (Griseb.) Clarke); × 0.2.—113. Isolectotype; *Luetzelburg 23955*.—114. Syntype; *Luetzelburg 23981*. Figures 119–130 were made from plants of this collection.

Each head is made up of structures having a variable branching pattern and containing the flowers. These groups are here called "fascicles." Details of their branching and concepts of the "spikelet" are discussed below.

The male flower consists always of only one stamen. The female flower is a single pistil with a trigonous straw-colored ovary and a rusty-brown style with three stigmatic branches (Fig. 116).

The apparently mature fruit is ellipsoidal to obovoid, 1.3–1.5 mm tall and 0.9–1.0 mm wide, with a dark brown apiculate apex and a bright straw-colored body with vertical grooves and three vertical ridges. The fruit has a shallow light green cupule at the base with three projections corresponding to the three ridges (Figs. 117–118).

As mentioned, the inflorescence is made up of 1–2 heads in the syntype collections. Each head is made up of fascicles which are more or less distinct bodies containing the last few branch orders. The fascicles are smaller and less distinct the more distally they arise in the head. In the basal fascicles of a head, one can distinguish without difficulty the subtending bract of the fascicle, its few-millimeters-long peduncle, and its prophyll. The apical fascicles are small and very crowded together; it is difficult to analyze them and find their subtending bracts and prophylls.

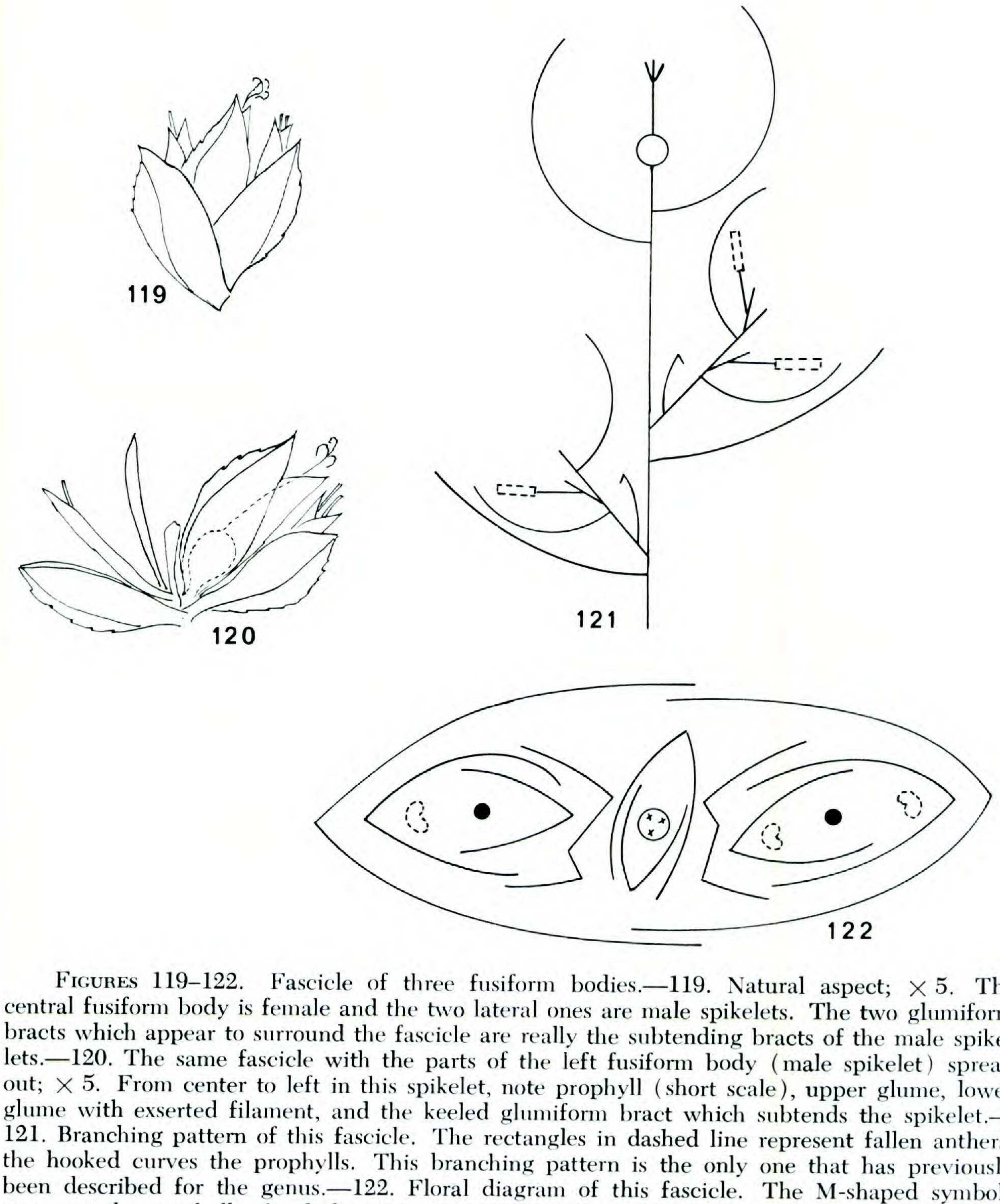


Figures 115–118.—115. Habit of a plant with two heads; × 0.4.—116. Pistil; × 19.—117. Fruit showing longitudinal grooves and basal cupule; × 19.—118. Fruit between its two apical free scales; × 8.

The internodes inside a head are very short, especially those inside a fascicle, so that the prophyll of an axis often appears to arise from the base of the adaxial surface of the subtending bract of that axis (Fig. 152). But while the bract arises from an axis of a certain branch order, the prophyll arises from the axis of the next higher branch order. The prophyll is a membranous laminule; on the lower-order axes it tends to be tubular in its basal part and surrounds the axis which bears it; on the higher-order axes the prophyll is open, flat and narrow.

On the lower internodes of a basal fascicle in a head where internodes are a few millimeters long, the prophyll visibly arises from its own axis separate from the subtending bract of that axis. But where the internodes are so short as not to be visible, it is necessary to use the order in which lateral organs arise, and to note which lateral organs are included in which others, in order to analyze the branching pattern. The presence of a morphologically distinct prophyll makes this possible.

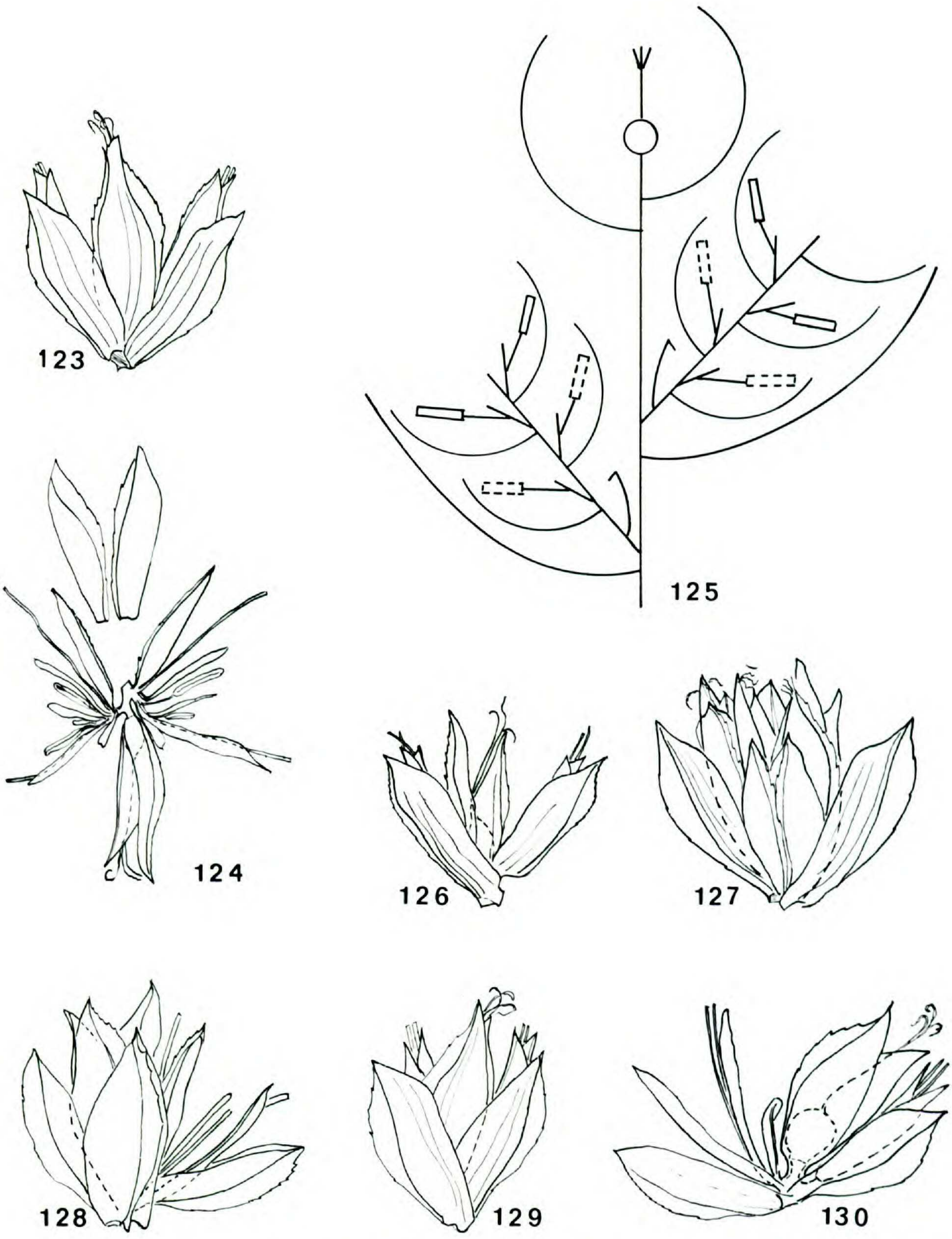
The structure of each fascicle is very variable, those at the base of a head having more elements. The fascicle is composed of 2–3 naviculate outer bracts 4.0 mm long, each with a toothed winged keel. As will be seen, these outer bracts are the subtending bract of the whole fascicle (if this bract remains attached to the fascicle when it is pulled out of the head), and the subtending bracts of the lowest side branches of the fascicle. These outer bracts surround



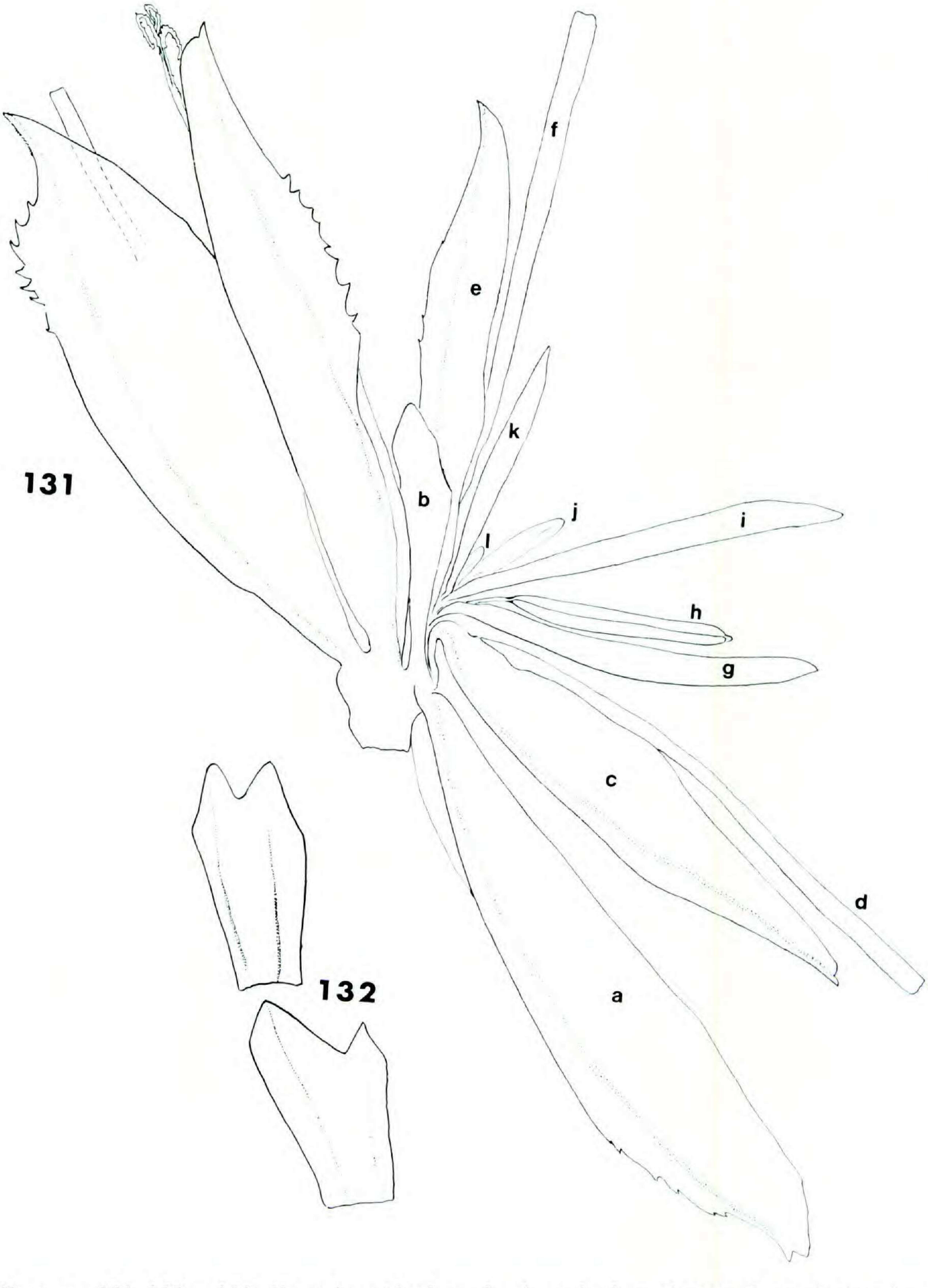
FIGURES 119–122. Fascicle of three fusiform bodies.—119. Natural aspect; × 5. The central fusiform body is female and the two lateral ones are male spikelets. The two glumiform bracts which appear to surround the fascicle are really the subtending bracts of the male spikelets.—120. The same fascicle with the parts of the left fusiform body (male spikelet) spread out; × 5. From center to left in this spikelet, note prophyll (short scale), upper glume, lower glume with exserted filament, and the keeled glumiform bract which subtends the spikelet.—121. Branching pattern of this fascicle. The rectangles in dashed line represent fallen anthers, the hooked curves the prophylls. This branching pattern is the only one that has previously been described for the genus.—122. Floral diagram of this fascicle. The M-shaped symbols represent the prophylls, the dark points the rachilla apices. (In the branching pattern diagrams a lateral axis is shown slightly separated from the bract in whose axil it arises. This slight separation is of course not an internode since the bract and the axis arising from its axil come from the same node.)

2–6 flat "fusiform bodies"; each body moves as a whole when pushed by a needle. Each fusiform body is surrounded by 1–2 glumiform, winged, naviculate bracts. Filaments and stigmas extend beyond the apices of the fusiform bodies.

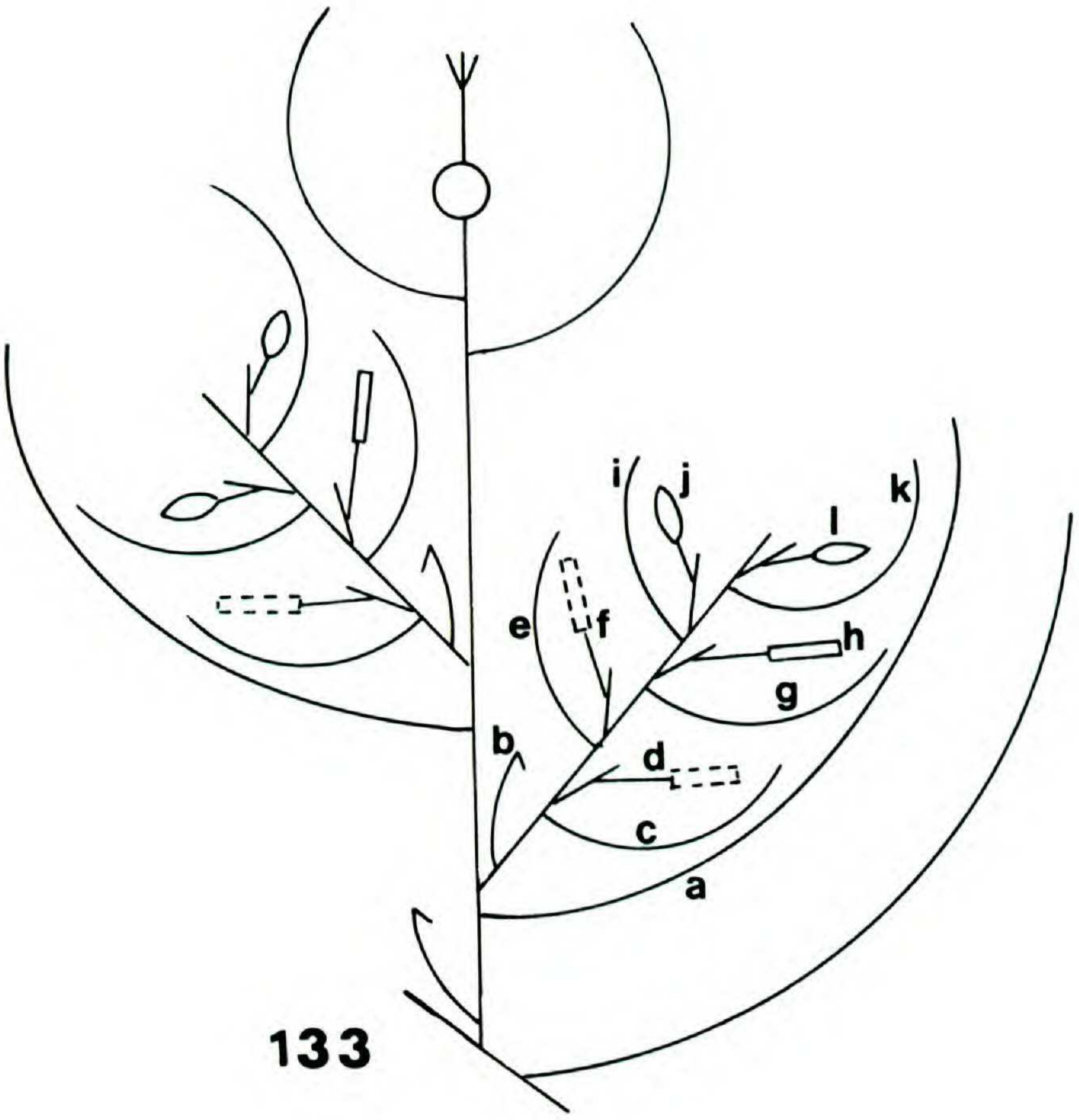
Several fascicles were extracted from various parts of single heads (Figs. 119, 123, 126–129, 135) and analyzed to determine the unit which could be considered the spikelet. A great variety of structures was found in the fascicles from heads



FIGURES 123–130. Fascicle types.—123. Natural aspect of a fascicle of three fusiform bodies, a central female and two lateral male bodies; × 5.—124. The same fascicle with the two keeled bracts removed (shown above, detached), and the parts of the two lateral fusiform bodies (male spikelets) spread out; × 5. The central fusiform body (containing the pistil) is here directed downwards.—125. Branching pattern of this fascicle. The rectangles in continuous line represent anthers which are present. The general pattern is the same as in Fig. 121.—126–130. Other fascicles of the same capitulum, showing variation in number of fusiform bodies; × 5.



FIGURES 131–132.—131. Fascicle with three fusiform bodies; that to the right has had its parts spread out; × 23. a = keeled glumiform bract which subtends the male spikelet; b = prophyll; c, e, g, i, k = glumes; d, f = filaments from which the anthers have fallen; h = stamen with mature anther; j, l = anthers of young stamens.—132. Dorsal view of two prophylls spread out, showing the retuse apex and two veins. (The prophyll of the fascicle as a whole, and the bract in whose axil it arose, shown in Figs. 133–134, are not shown in this figure.)



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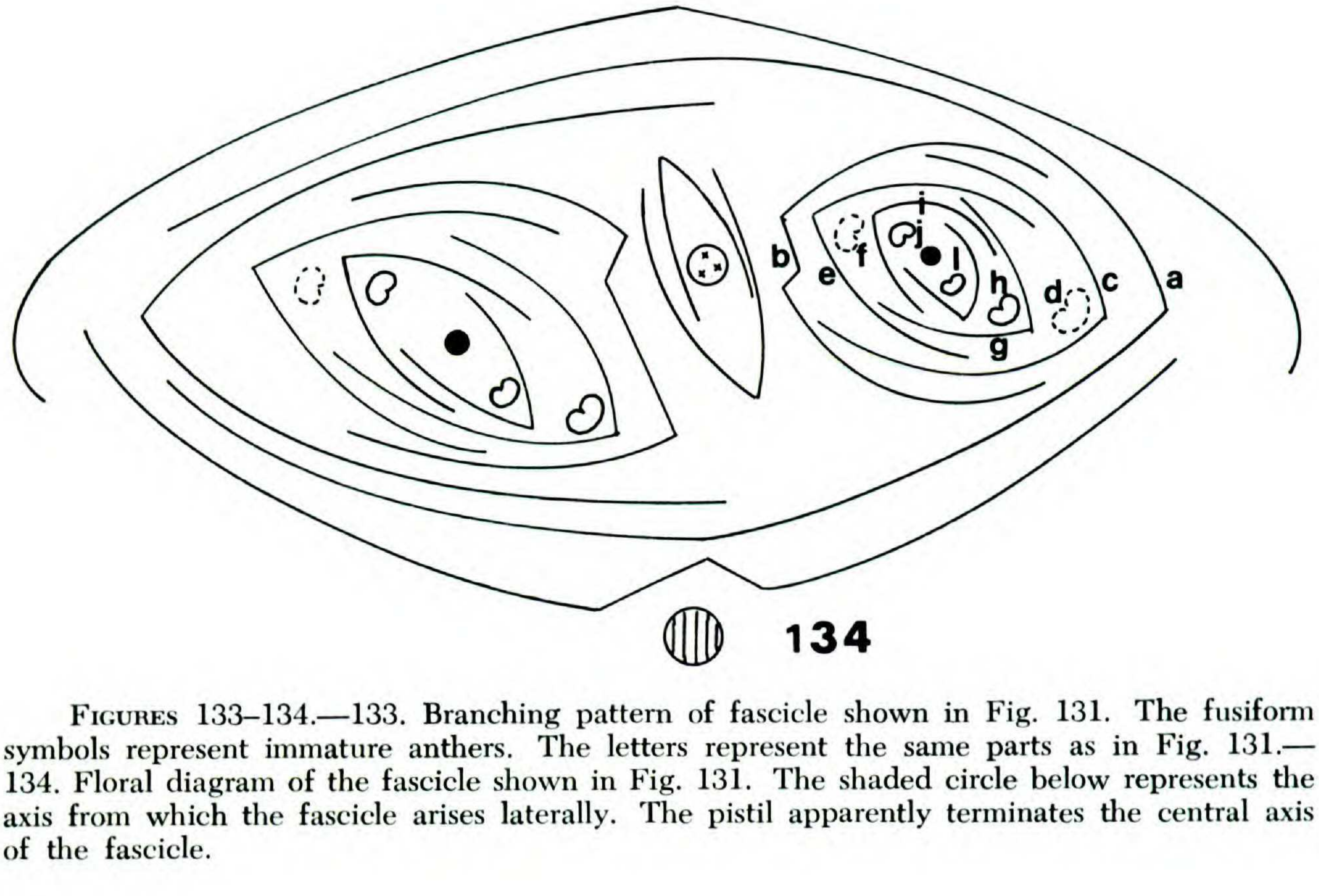

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FIGURES 133–134.—133. Branching pattern of fascicle shown in Fig. 131. The fusiform symbols represent immature anthers. The letters represent the same parts as in Fig. 131.—134. Floral diagram of the fascicle shown in Fig. 131. The shaded circle below represents the axis from which the fascicle arises laterally. The pistil apparently terminates the central axis of the fascicle.

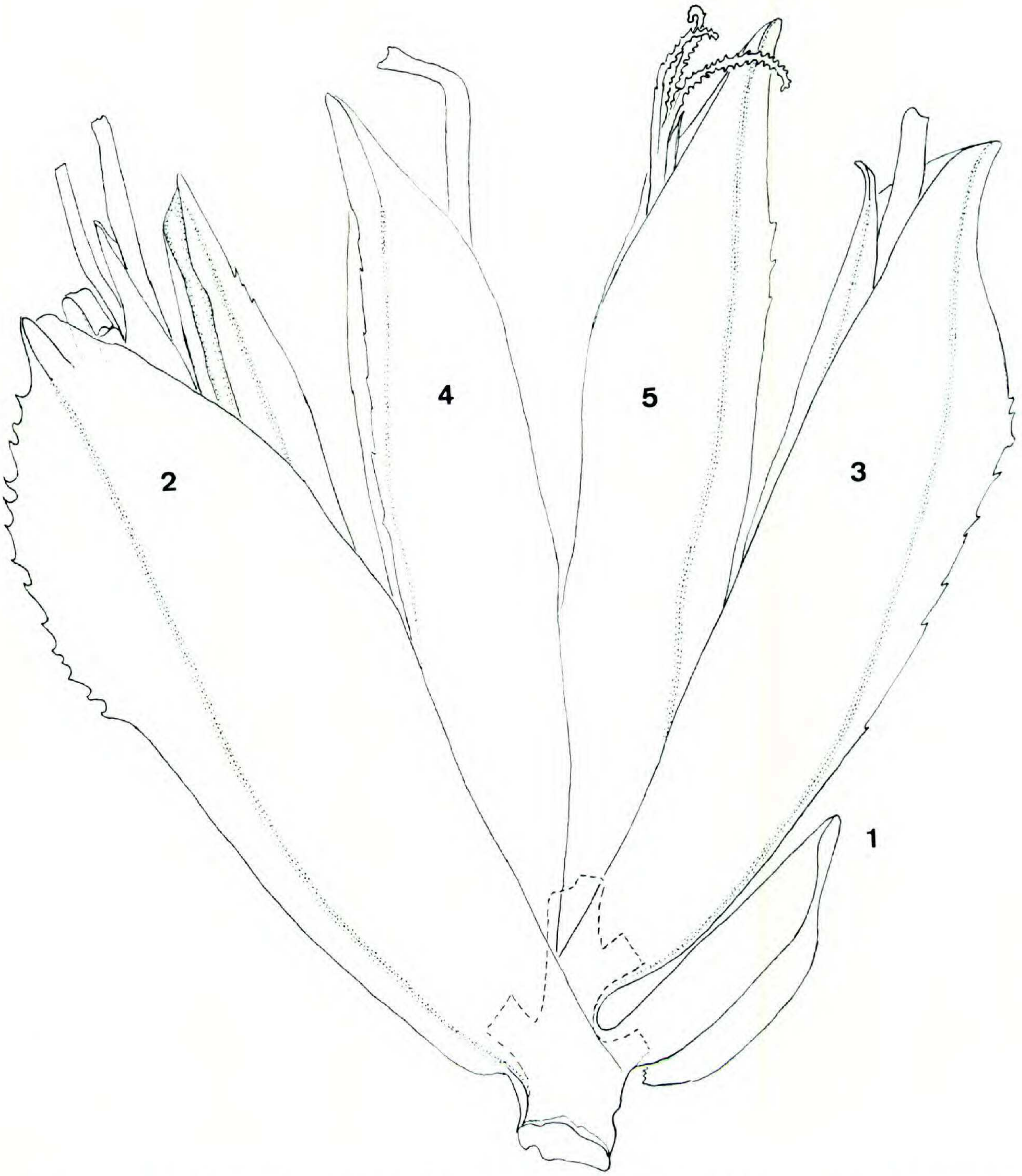
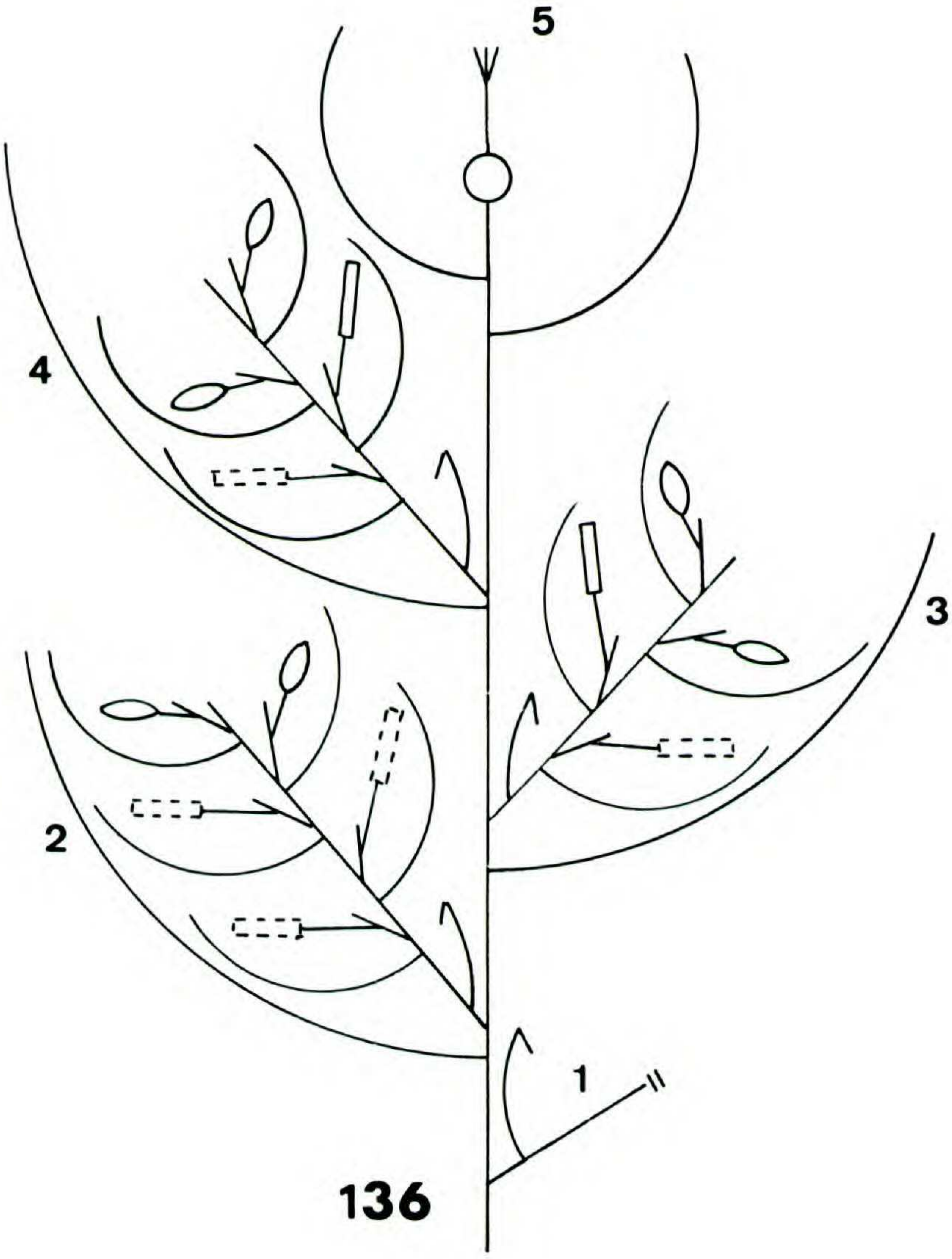


FIGURE 135. Natural aspect of a fascicle of five fusiform bodies; × 29. The fusiform body to the right (no. 1) and its subtending bract were removed; only its prophyll remains in this drawing. The axis of the fascicle and its branches (rachillae) are shown in dashed outline.

of the two collections when these were opened out and examined (Figs. 120, 124, 130–132, 152). The branching patterns found are given in Figs. 121, 125, 133, 136, 138–151. For a few of the fascicles the floral diagram is also given (Figs. 122, 134, 137, 153). Each bract, glume, scale, prophyll, stamen and pistil shown was actually seen. The internode lengths in these diagrams, as in all diagrams of branching pattern in this paper, are exaggerated for greater clarity, so as to show better to which axes the various parts are attached.



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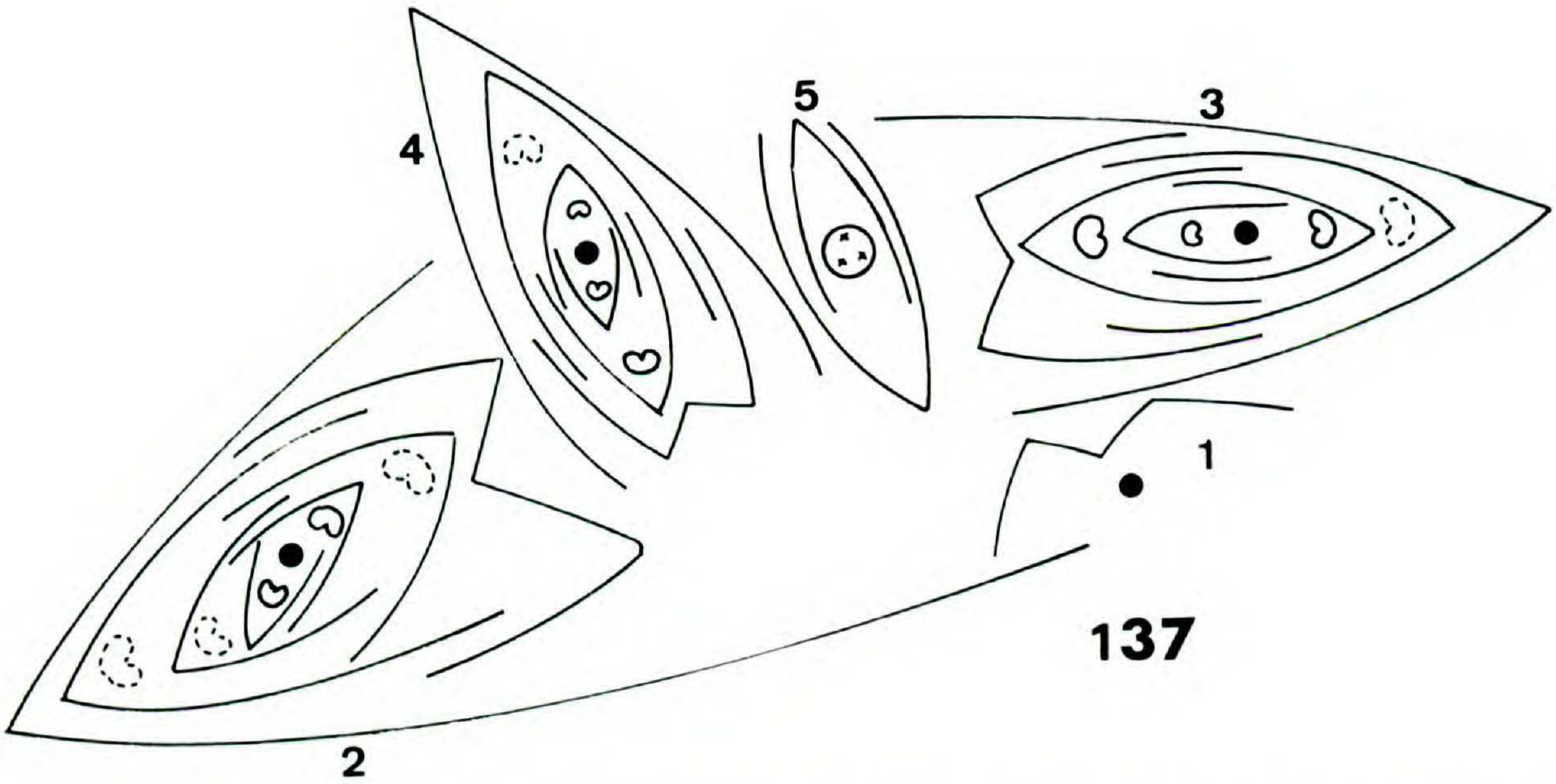

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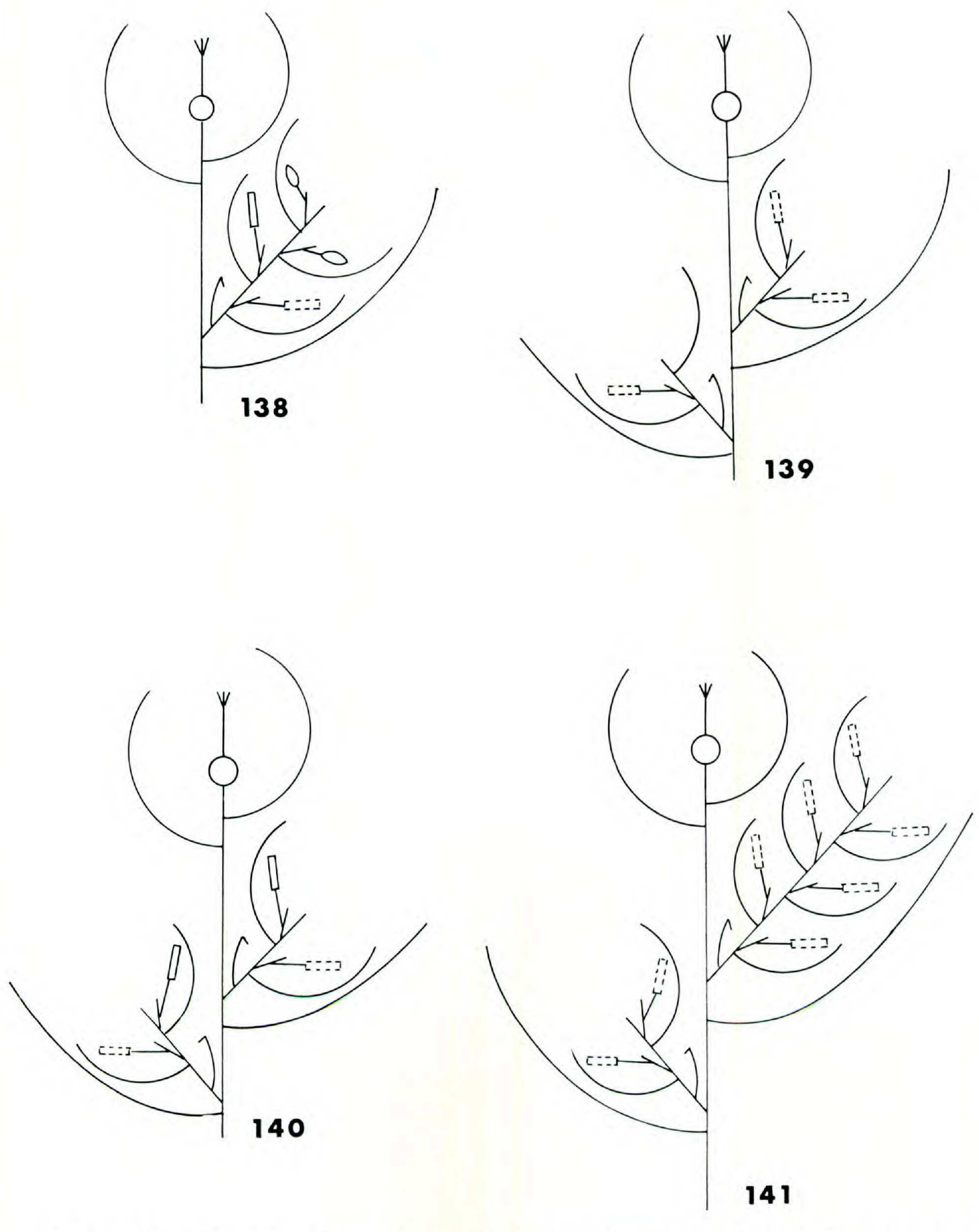
FIGURES 136–137.—136. Branching pattern of fascicle shown in Fig. 135. The numbers represent the same fusiform bodies as in that figure.—137. Floral diagram of fascicle shown in Fig. 135. The parts of fusiform body no. 1 are not shown except for the prophyll.



FIGURES 138–141. Branching patterns of other fascicles examined.—138. Fascicle of two fusiform bodies: one female made up of a pistil and its two free scales, and one male which is a spikelet of male monandric flowers with its prophyll and subtending bract.—139–141. Fascicles of three fusiform bodies: one central female and two lateral males. Note variation in stamen (i.e., male flower) number.

In general, a fascicle has a central axis which arises in the axil of a bract (the bract is glumiform in the distal fascicles in a head), a small membranous prophyll (almost imperceptible in the distal fascicles) as its basal lateral organ, 1–4 side branches, and at the apex two free, winged, naviculate scales surrounding a pistil. Each side branch from the central axis arises in the axil of a glumiform bract and possesses a prophyll. The parts which these side branches bear vary in nature and number. The following structures were found making up the side branches: (1) single axis with prophyll and 1–9 glumes, each glume subtending a male flower of a single stamen or sometimes the distal glume empty (Figs. 121, 125, 133, 136, 138–148, 149 upper left side axis); (2) single axis with 2 or 4 scales, the two basal ones (when there are four) are empty and the two distal ones are always free (not fused by their edges) and surround an apparently terminal pistil (lowest side branch in Figs. 142–143, 145; lowest two side branches in Figs. 146–148); (3) a side axis which itself is branched. In these, the side axis terminates in a pistil surrounded by two scales; each of its own 1–2 lateral branch axes arises in the axil of a bracteole and has a prophyll and 1–2 glumes, with each of these glumes subtending a male flower of one stamen, or the upper empty (the two lower side branches in Fig. 149; lower side branch in Fig. 150; both side branches in Fig. 151).

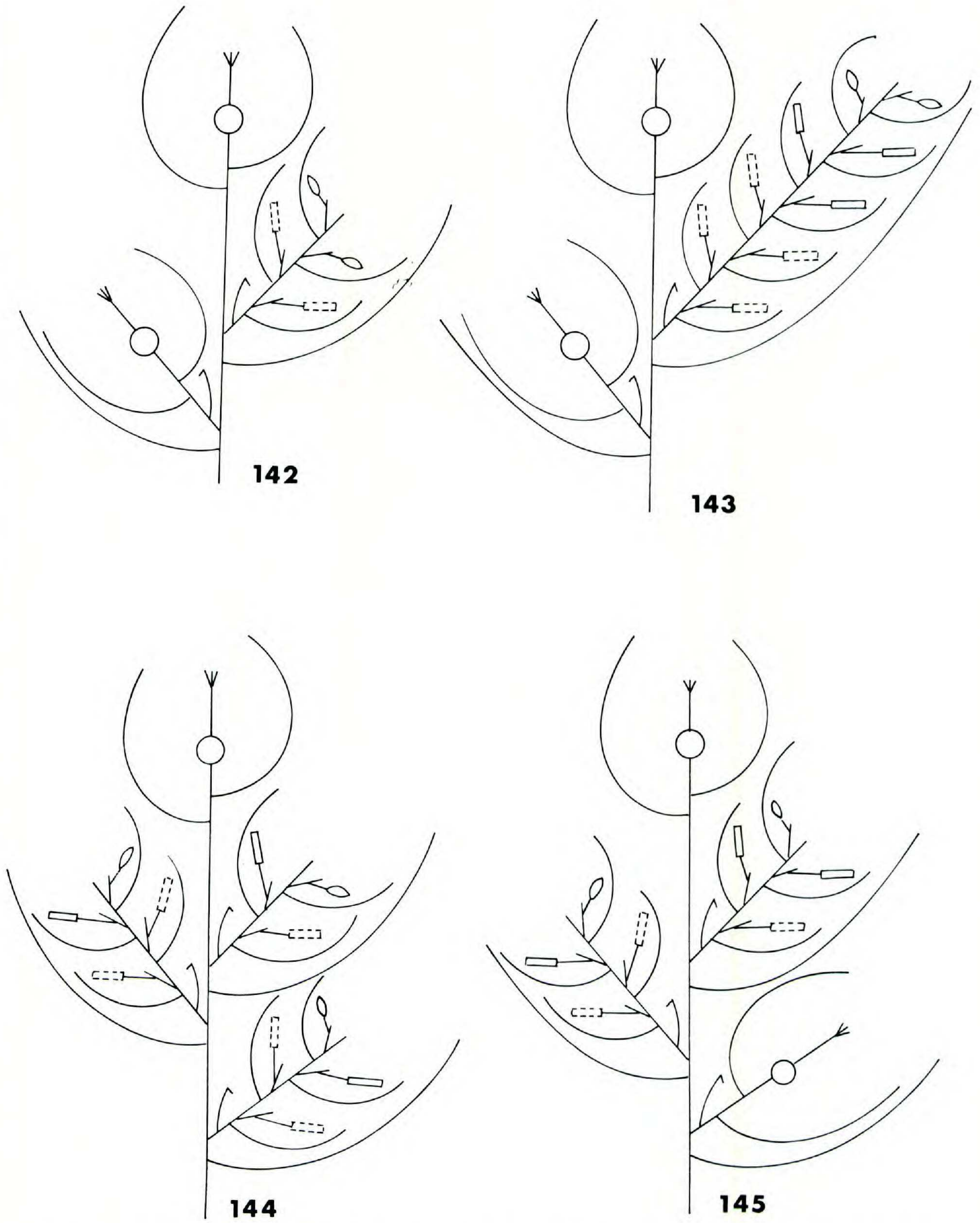
I consider a "spikelet" a structure composed of a single axis of theoretically indefinite growth, bearing lateral sessile flowers in the axils of bracts called "glumes." In the plant here studied, the structures containing the male flowers are clearly spikelets. I do not include the subtending bract or the prophyll in the definition of the spikelet. The axis bearing the pistil is apparently of definite growth since the pistil appears to be terminal and I have indicated this in the branching pattern diagrams. I believe, however, that all flowers in the Cyperaceae are fundamentally lateral and that those that appear terminal on the rachilla are really only pseudoterminal, as is clearly true in 1-flowered spikelets of *Cyperus* (sensu lato), *Eleocharis*, etc. But until I have direct proof or at least an indication that the pistil in *Bisboeckelera* and *Diplacrum* is really lateral, I do not wish to consider this terminal portion of the axis with its scales and pistil a spikelet. I use the term "scale" here since I reserve the term "glume" for the lateral laminar organs of what I consider a true spikelet.

In three cases seen, the central axis of the fascicle did not terminate in a pistil but merely stopped, and just below its tip gave rise to two lateral branches, each arising in the axil of a keeled bract and provided with a prophyll at its base. These branches were either simple and terminated in a pistil with its two scales (Fig. 150, upper side branch), or were compound with 1–2 lateral basal branch axes arising in the axils of bracteoles and possessing a prophyll, glumes and male flowers of one stamen each (Fig. 150, lower side branch; 151, both side branches).

Of 18 fascicles analyzed, in 10 the central axis was wholly contained in the fascicle, that is, the prophyll of that axis and its subtending bract had separated from the inflorescence as part of the fascicle. In the remaining 8 cases the fascicle contained only the upper part of the main axis; its base remained with the rest of the head so that its prophyll and subtending bract were not found in the detached fascicle.

This analysis showed:

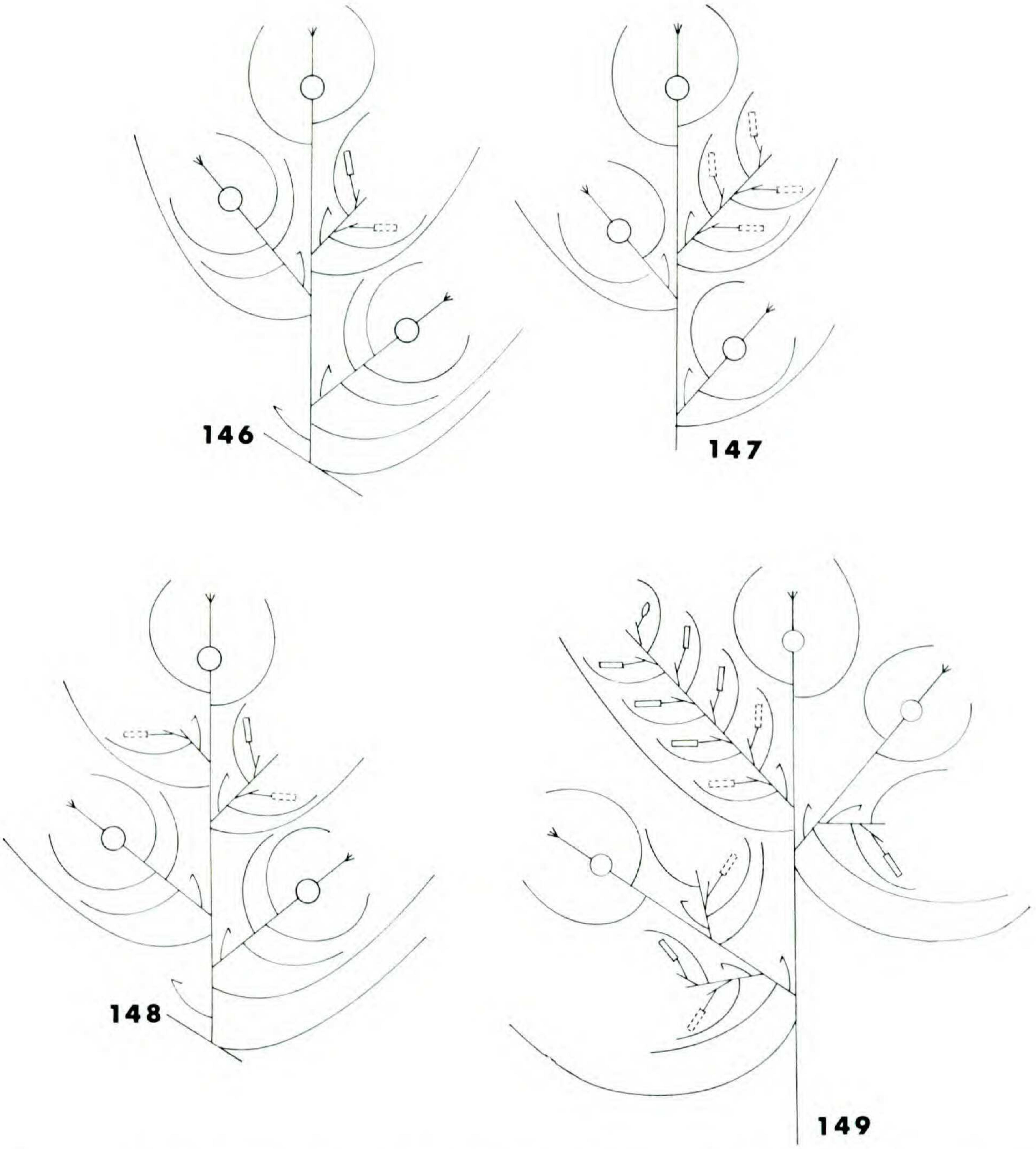
1. All axes of the inflorescence arise in the axils of bracts and have a prophyll as the first basal lateral organ.



FIGURES 142–145.—142–143. Fascicles of three fusiform bodies: one central female and two laterals of which one is female and the other male.—144. Fascicle of four fusiform bodies: one central female and three lateral males.—145. Fascicle of four fusiform bodies: one central female, two lateral males, and one lateral female.

2. The ends of the branches of the inflorescence, that is, those axes which do not branch anymore, form the rachillas of spikelets of 1–9 single-stamen male flowers, or bear 2 or 4 scales and apparently terminate in a pistil.

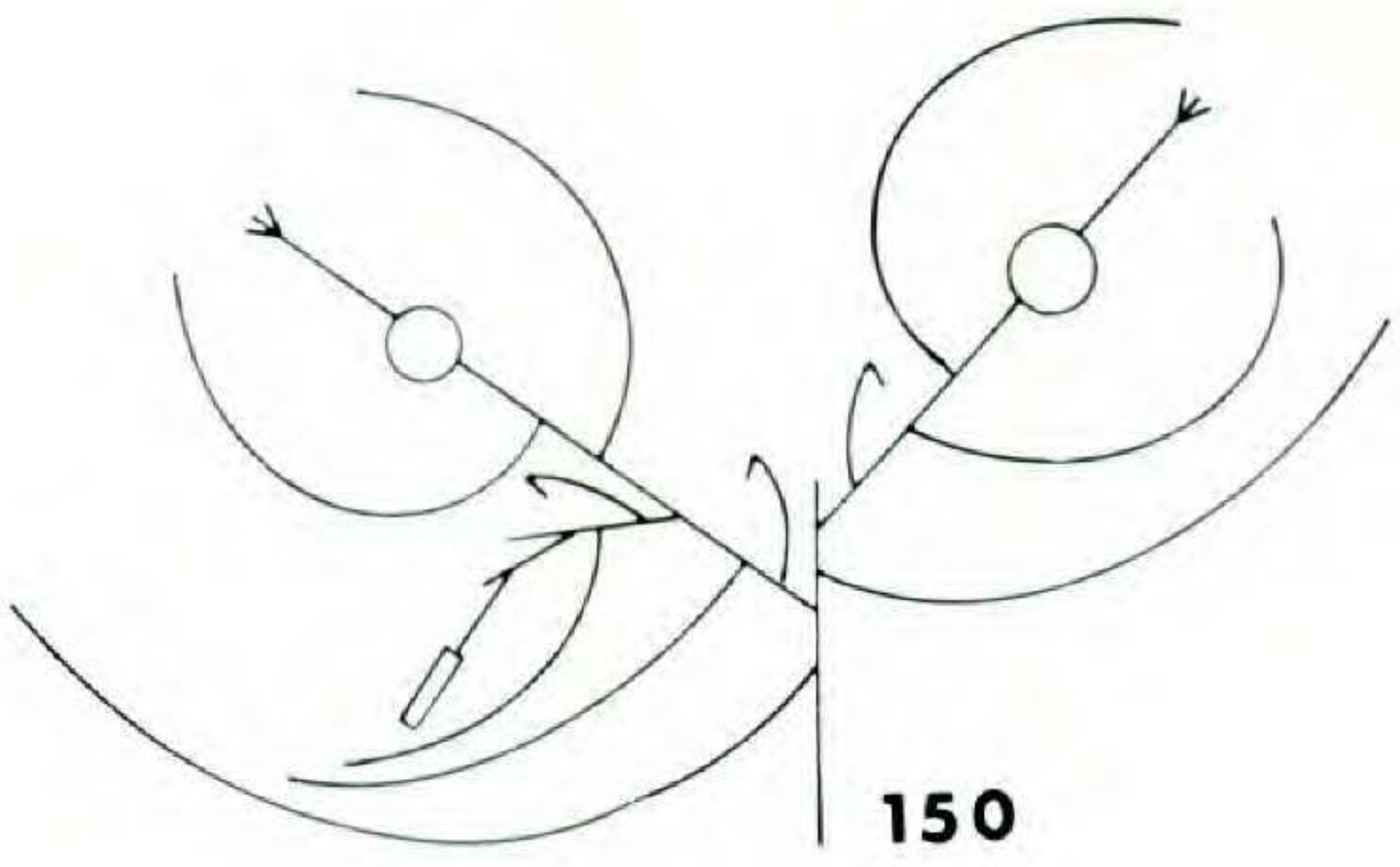
3. All the scales are free, including the two which surround the pistil. There



FIGURES 146–149. Fascicles of four fusiform bodies.—146–147. Fascicles with one central female, one lateral male and two lateral female bodies. Note that the lateral female bodies may have two or four scales.—148. In this fascicle the central fusiform body is bisexual since it is made up of the pistil on the central axis and its two scales *plus* the most distal lateral male spikelet of one flower and its prophyll and subtending bract. Each of the other three lateral branches forms a separate fusiform body.—149. Fascicle with one central female, one lateral male (a many-flowered spikelet), and two lateral bisexual fusiform bodies. The latter two are themselves branched, the branches being reduced male spikelets.

is no formation of a utricle even though the two scales which cover the pistil arise at almost the same level.

4. The ultimate "units" of the inflorescence, made up of axes of the last few branch orders and the lateral organs they bear, can only be delimited based on the branching pattern, not based on spatial individuality. For example, the "fusiform bodies," which are the smallest units more or less spatially distinct one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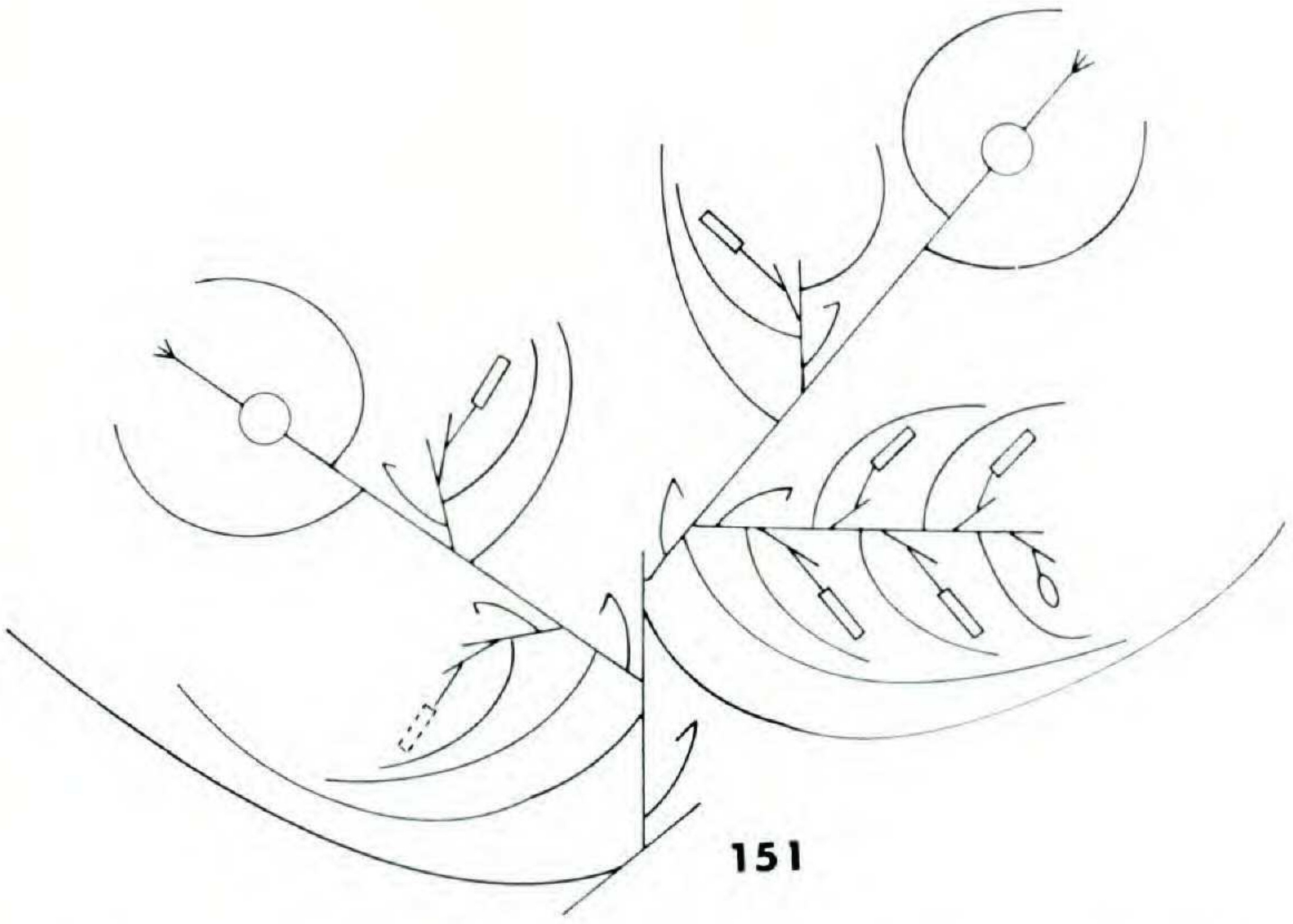
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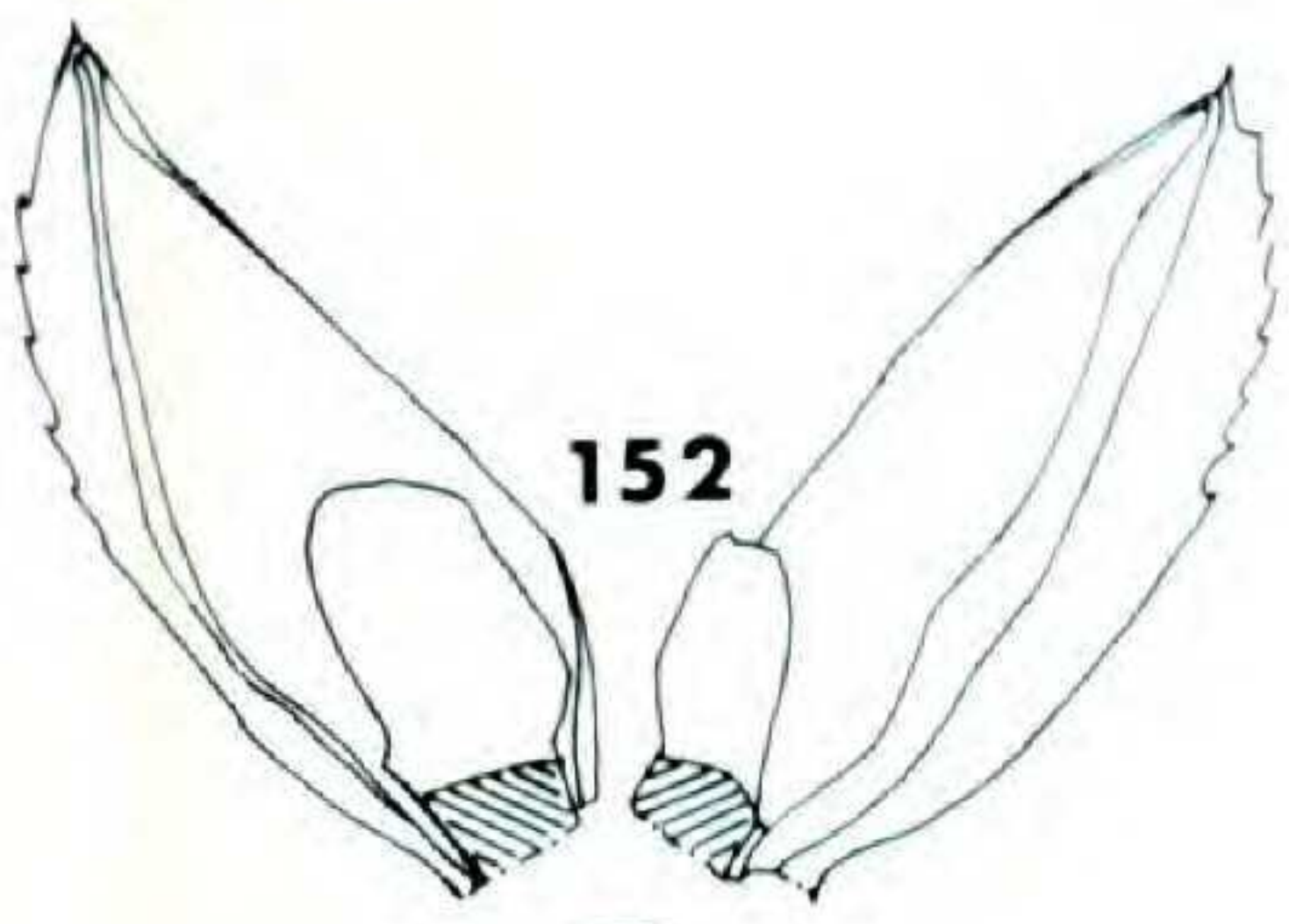
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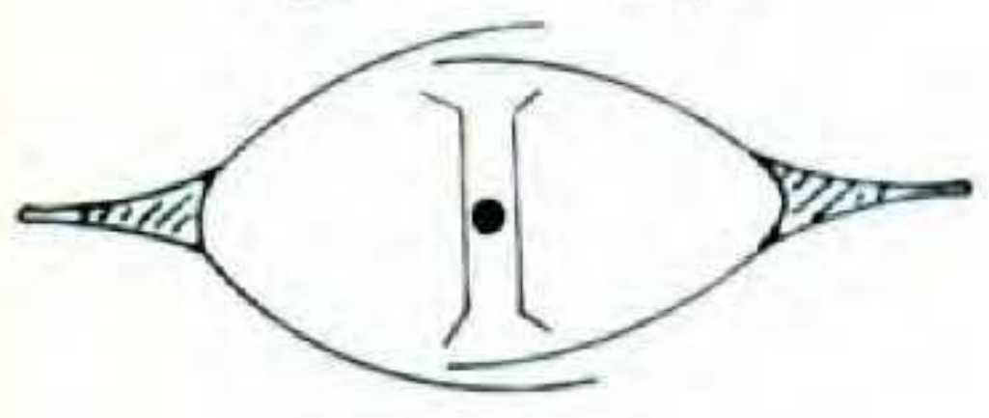
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FIGURES 150–153. Fascicles without a central terminal female fusiform body, only two lateral bodies.—150. Branching pattern with one body female and one bisexual.—151. Branching pattern with both lateral bodies bisexual.—152. Fascicle with the upper part of the two lateral branches removed and the central axis split; × 6. The two keeled subtending bracts of the branches and their prophylls are shown. The prophylls arise from an axis of higher order than that from which the subtending bracts arise (see Figs. 150–151).—153. Cross section of this fascicle.

from the other, cannot be considered the ultimate units of the inflorescence. The organization of a fusiform body is very variable; its axis may be simple or itself branched and the number of pistils and male spikelets it contains is not constant.

5. It is of course possible to define only two types of ultimate inflorescence units in this genus: (a) a male unit consisting of a male spikelet, and, if one wishes, also the prophyll and subtending bract, and (b) a female unit consisting of the tip of an axis with a pistil and the two scales below it. (When there are four scales below the pistil, the lower two should not be considered part of this female unit since in many cases, such as those shown in Figs. 149 and 151, these two lower scales subtend male spikelets.) However, traditionally, the "spikelet" of *Diplacrum* in taxonomic descriptions includes both the male and female parts. The description given here shows how much this can vary in even one head.

After having examined the inflorescence units and the vegetative characters of *Luetzelburg 23981* and *23955*, I can state with confidence that these collections are *Diplacrum longifolium* (Griseb.) Clarke and not a new species of *Bisboeckelera* as Süssenguth thought. In *Bisboeckelera* the female flower is always inside a utricle while in *Diplacrum* the scales that surround the pistil are free and do not form a utricle. Thus, *Bisboeckelera paporiensis* is a synonym of *Diplacrum longifolium.* Koyama (1967) also noted this synonymy but did not give the reasons to justify his decision.

Süssenguth (1943) called the *spikelets* of male flowers with one stamen a "male flower." Probably he examined only one spikelet with three stamens for he wrote: "Flor masculus tristaminatus."

It is strange that Süssenguth did not see that this material belongs to the genus *Diplacrum.* He thought it similar to *Bisboeckelera* and compared the specimens to the illustration of *Hoppia irrigua* Nees (= *Bisboeckelera irrigua* (Nees) O. Ktze) in Plate 136 of Clarke (1909). He saw that the specimens were not *B. irrigua* because of the absence of a utricle and because the leaves in the specimens were much narrower. Plates 134 and 135 of this same book of Clarke are species of *Diplacrum* but these were not cited by Süssenguth. The "spikelet" of *Diplacrum longifolium* illustrated in Plate 135 is identical to that described by Süssenguth for *Bisboeckelera paporiensis.* But he did not recognize that Luetzelburg's collections were of the same species as the plant in Plate 135, probably because the Luetzelburg plants have only 1–2 small heads per flowering culm while the plant in Plate 135 is more robust with 4 large heads per culm.

Certain that his specimens belonged to *Bisboeckelera,* Süssenguth described the new species *B. paporiensis,* and established for this species a new section of the genus, *Bibractearia,* to contain species of the genus having the pistil enclosed in two free scales and not in a utricle.

Koyama (1967) recorded only two species of *Diplacrum* for the New World, *D. capitatum* (Willd.) Boeck., widely distributed in the tropical region, and *D. guianensis* (Nees) Koyama of southern Venezuela and the Guianas. These two species are easily separable by the surface texture and color of the fruits and by the size of the keeled glumiform bracts. Koyama & Oldenburger (1971) registered the presence of the very different looking *Diplacrum africanum* Clarke in Surinam. In 1965 I had also noted this species in Brazil (Amapá, perto da cidade de Amapá, 29 Aug. 1955, *Black 55-18535.* Maranhão, perto de Carolina, campo cerrado, 26 May 1950, *Pires & Black 2247*), although I did not publish on it. In fact, Gross had previously annotated the Pires & Black collection as this species. In his monograph of the American species, Koyama used the name *D. capitatum* (Willd.) Boeck. instead of *D. longifolium* (Griseb.) Clarke, because the epithet *capitata* is older. However, I prefer to continue using *longifolium,* the epithet accepted by all cyperologists, until the type of *Scleria capitata* is identified beyond all doubt.

Besides Luetzelburg's two collections, I have studied 13 more collections of *D. longifolium* from Venezuela and Brazil. Even this small number was enough to show great variation in the characters usually used to separate species and varieties in this complex (Figs. 154–155). The following characters may be noted:

Number of heads per culm, 1–7; width of leaves, 1.5–10.7 mm; width of keel (wing) of the scales which enclose the fruit, 0.2–1.3 mm; length of basal leaves,

FIGURES 154–155. Habits of plants of other collections of *Diplacrum longifolium* (Griseb.) Clarke showing variation in number of capitula per culm; × 0.3.—154. *Ule 7671*, culm with seven capitula.—155. *Pires et al. 6305*, with 1–2 capitula per culm. This collection has a habit similar to the types of *Bisboeckelera paporiensis*.

22–70 cm; length of the basal bract of the inflorescence (cauline leaf), from (5.5–)22 cm to more than 60 cm; surface of mature fruit smooth, lightly wrinkled, or heavily wrinkled.

The correlation of characters is not sufficiently high among the collections studied, and there are no gaps in the variation pattern, so that it is not possible to divide the complex into species or varieties. Also, there is no correlation between the morphology and the geography.

Other collections studied (det. L. T. Eiten):
Diplacrum longifolium (Griseb.) Clarke

VENEZUELA. AMAZONAS: Río Atabapo (Río Orinoco), Cano Teni, 18 Oct. 1950, *Maguire 29275* (IAN).

BRAZIL. AMAPÁ: Calçoene, 21 Aug. 1962, *Cavalcante 52562* (IAN). PARÁ: Belém, 27–30 June 1944, ***Baldwin Jr. 4542*** (IAN). Belém, Buçuguara, 14 Oct. 1945, ***Pires & Black 410*** (IAN). Rio Moju, Fábrica, 31 May 1954, *Black 54-16257* (IAN). Colares, 29 Sep. 1954, ***Black s.n.*** (IAN). Região de Anapu, Rio Tapacu, Portel, 10 May 1956, *Fróes 32785* (IAN). Serra do Cachimbo, 425 m, 15 Dec. 1956, *Pires et al. 6305* (IAN). Região de Ariramba, mata a leste do acampamento do Jamacuru, 2 June 1957, *Black et al. 57-19843* (IAN). RORAIMA: Rio Branco pr. Serra Pelada, Oct. 1908, *Ule 7671* (IAN). AMAZONAS: Manaus, Flores, June 1910, *Ule 8817* (IAN). GOIÁS: Varedão do Relâmpago, duas léguas de Carolina, 28 May 1950, ***Pires & Black 2394*** (IAN). SÃO PAULO: Campo de Itirapina, 24 Jan. 1951, ***Black 51-11317*** (IAN).

MICROPAPYRUS VIVIPAROIDES Süss.

Description of holotype of *Micropapyrus viviparoides* Süss., Bot. Jahrb. Syst. 73: 116–117. 1943: Brasilia septentrionalis, Civitas Alta Amazonas, Rio Negro, San Felippe, sandiger Ufer in Urwald, 16 Oct. 1928 *Luetzelburg 22381* (M).

The plant is delicate, forms clumps 16–22 cm tall with several erect leafless cylindrical or slightly flattened culms (peduncles) 6–17 cm long and 0.3–0.5 mm wide (Fig. 156). Just below the inflorescence the culm is angular, scaberulous on the angles, rarely also on the faces. The leaves are all basal and form tufts. The leaf sheath is 5–7 mm long; on the laminar side of the sheath (the side which bears the blade) the visible longitudinal nerves are close together; the contralaminar side of the sheath is membranous and thin-textured. The leaf blade is 5–7 cm long and 0.7–1.0 mm wide at the base, narrowly linear, gradually narrowing to the apex, the ventral surface concave, margins and midvein (sometimes also the lateral veins) scaberulous. The lowest bract of the inflorescence is leaflike, up to 1.5 cm long.

The inflorescence is a delicate anthela of 3–7 rays 1–8 cm long (Fig. 157). Each ray is a sympodial axis. The rays arise at the tip of the peduncle separated by very short internodes. Each ray is subtended by a bract. The base of the ray is swollen and surrounded by a tubular prophyll. The prophyll is 3.5 mm long with an oblique mouth and has two short pointed extensions on the adaxial side of the apex (sometimes these appear to be on the abaxial side due to torsion).

The rays bear pseudospikelets, very tiny vegetative shoots, and groups made up of both of these structures. (Details are given below.)

The pseudospikelet is fusiform and elliptical, 2.8–3.5 mm long and 0.45 mm wide; it has a short pedicel. The number of glumiform bracts in a pseudospikelet is 3–4 (rarely 5) (Figs. 158–161, 163–164). The first or lower glumiform bract is always empty; the second is never empty but covers a pseudanthium (a structure that looks like a bisexual flower but in this species is made up of a short axis or rachilla, bearing laterally two male flowers of one stamen each and an apparently terminal female flower of a single pistil). The third glumiform bract usually covers a pseudanthium but sometimes is empty. The fourth and fifth glumiform bracts when present are always empty. The pseudospikelets that terminate a ray (rarely one along a ray) are generally associated with a tiny vegetative shoot which arises in the axil of the glumiform bract that is immediately below the basal bract of the pseudospikelet.

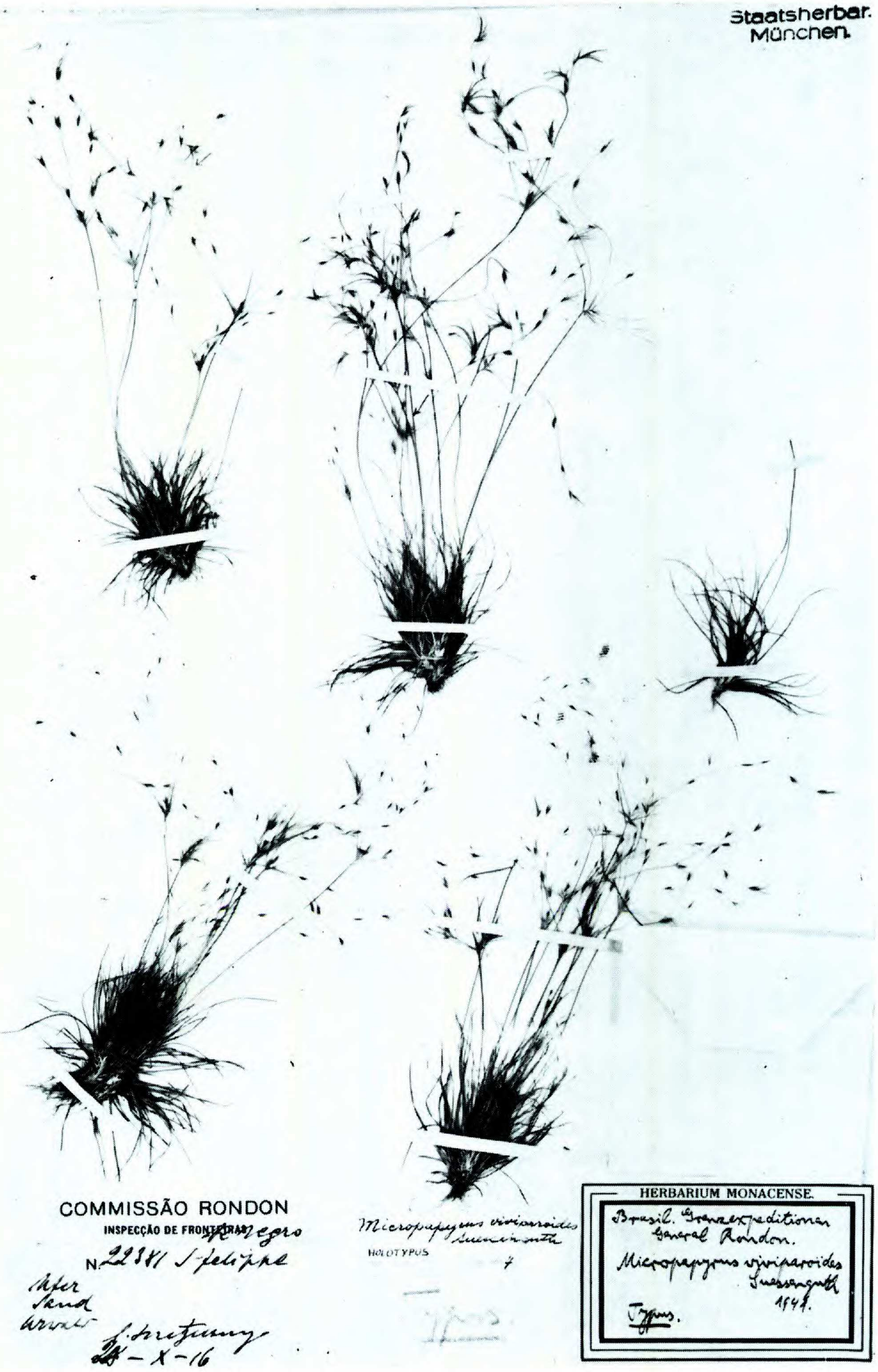


FIGURE 156. Holotype sheet of *Micropapyrus viviparoides* Süss.; *Luetzelburg* 22381; × 0.4. Figures 157–164 are from plants of this sheet.

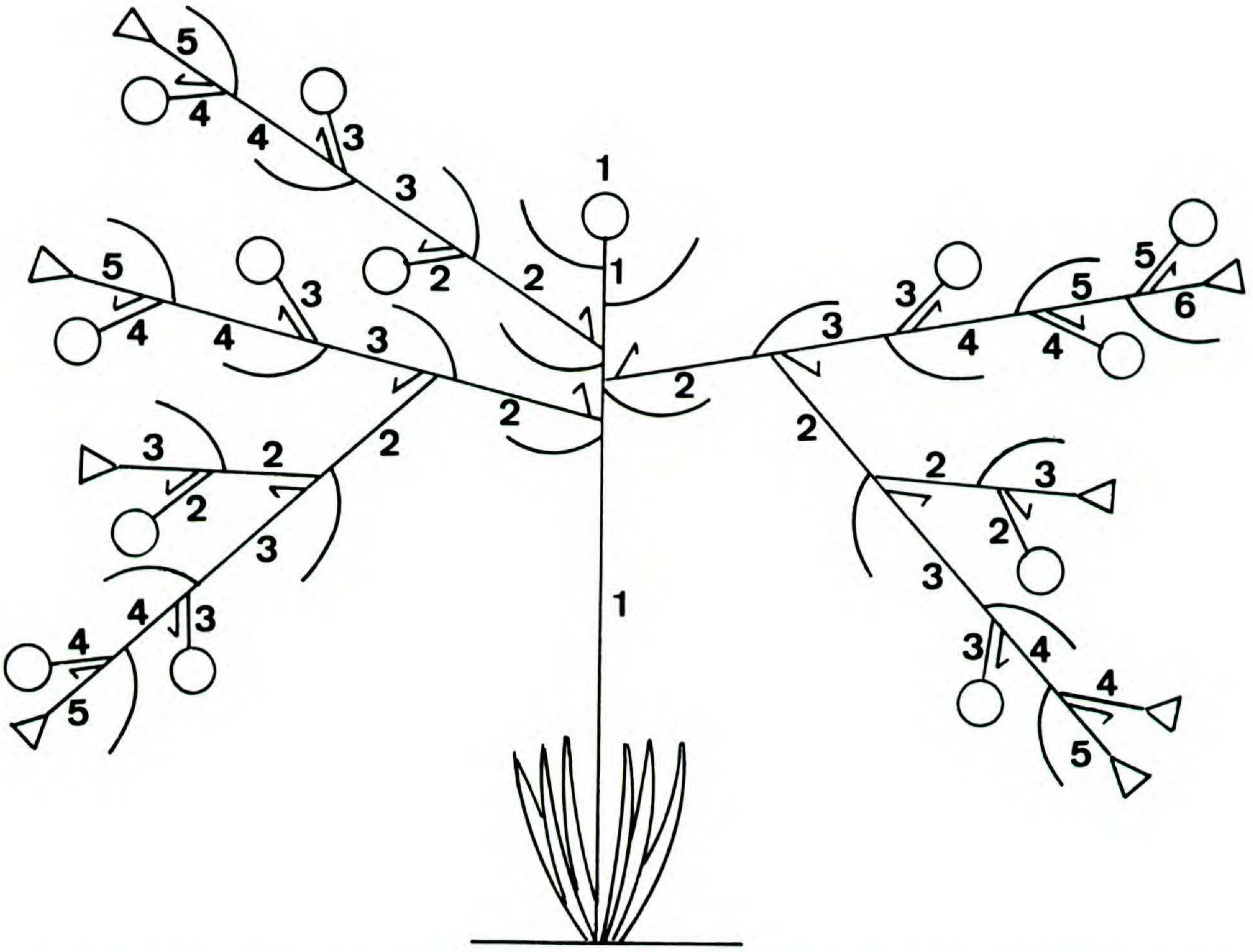


FIGURE 157. Branching pattern of an actual plant examined. The branching orders are represented by numbers. The curved lines represent bracts, the short hooked lines the prophylls. Circles indicate pseudospikelets and triangles vegetative shoots. Axis no. 1 is the culm (peduncle) from whose apex the rays of the inflorescence arise and which continues on to form the axis of the terminal pseudospikelet. This axis is monopodial. The rays and subrays are sympodial, that is, formed of the first two basal internodes of successively higher-order branches. (For reasons of clarity, a newly arisen axis is shown slightly separated from the bract in whose axil it arises. This slight separation is of course not to be considered an internode. The slight separation along an axis from its origin to its prophyll is, however, a genuine internode (the subprophyllar internode).)

The pseudanthia do not emerge from the pseudospikelet axis (rachis) at the nodes, that is, in the axils of the glumiform bracts. They emerge, that is, physically separate from the axis, in the middle or upper part of the internode. However, morphologically, the pseudanthium axis (rachilla) has its origin at the same node as the glumiform bract immediately below it; its axis grows adnate or concrescent to the pseudospikelet rachis (phenomenon of "concaulescence," Troll, 1964: 127–129), and only separates above (Figs. 160, 163–164).

In the pseudanthium, the female flower is always apparently terminal on a stipe 0.2–0.4 mm long. It consists of a single pistil with two stigmatic branches and is surrounded at the base by three smooth sinuous bristles. The stipe has two male flowers which arise at different levels (Figs. 160–164).

The fruit is ovoid-apiculate, short-stipitate, 1.6–2.0 mm long (including the apical point and the stipe) and 0.35–0.6 mm wide (Figs. 160–161).

The branching pattern of the whole inflorescence of this plant merits a full presentation (Fig. 157). The peduncle (culm) does not bear cauline leaves; it acts as the lowest internode of the first-order axis of the inflorescence. At its tip arise the several rays of the inflorescence, 3–7 in the plants examined. Each ray arises at a node and is separated from the node of the next ray by a very short internode. Since there are 3–7 rays, the number of internodes is 2–6. Immediately above the uppermost ray is a pseudospikelet, or this is separated from the uppermost ray by 1–2 nodes with glumiform bracts. Thus 1–3 internodes intervene between the node of the uppermost ray and the node where the lowermost bract of the pseudospikelet arises. The pseudospikelet on the tip of the peduncle has 3 (very rarely 4) internodes, one between each two consecutive bracts.

Each ray which directly arises from the peduncle has as its basal internode the first internode of a second-order axis (branch of the peduncle). This first internode is very short and ends at the node bearing the prophyll of the second-order branch, that is, it is a subprophyllar internode. The branch continues with a second internode which because it is longer and visible appears to be the first or basal internode of the ray. The ray continues with its third internode being the first internode of a third-order axis. This is also short and terminates at a node with a prophyll. This third-order branch then continues with a longer visible internode that appears to be the second internode of the ray although it is really the fourth, etc. Thus, the ray is made up of a single line of the first two internodes of branches of successively higher order. Each short internode of the ray (i.e., the beginning of each new branch) is subtended by a bract and ends at a node with a prophyll. In other words, the growth of the ray is sympodial.

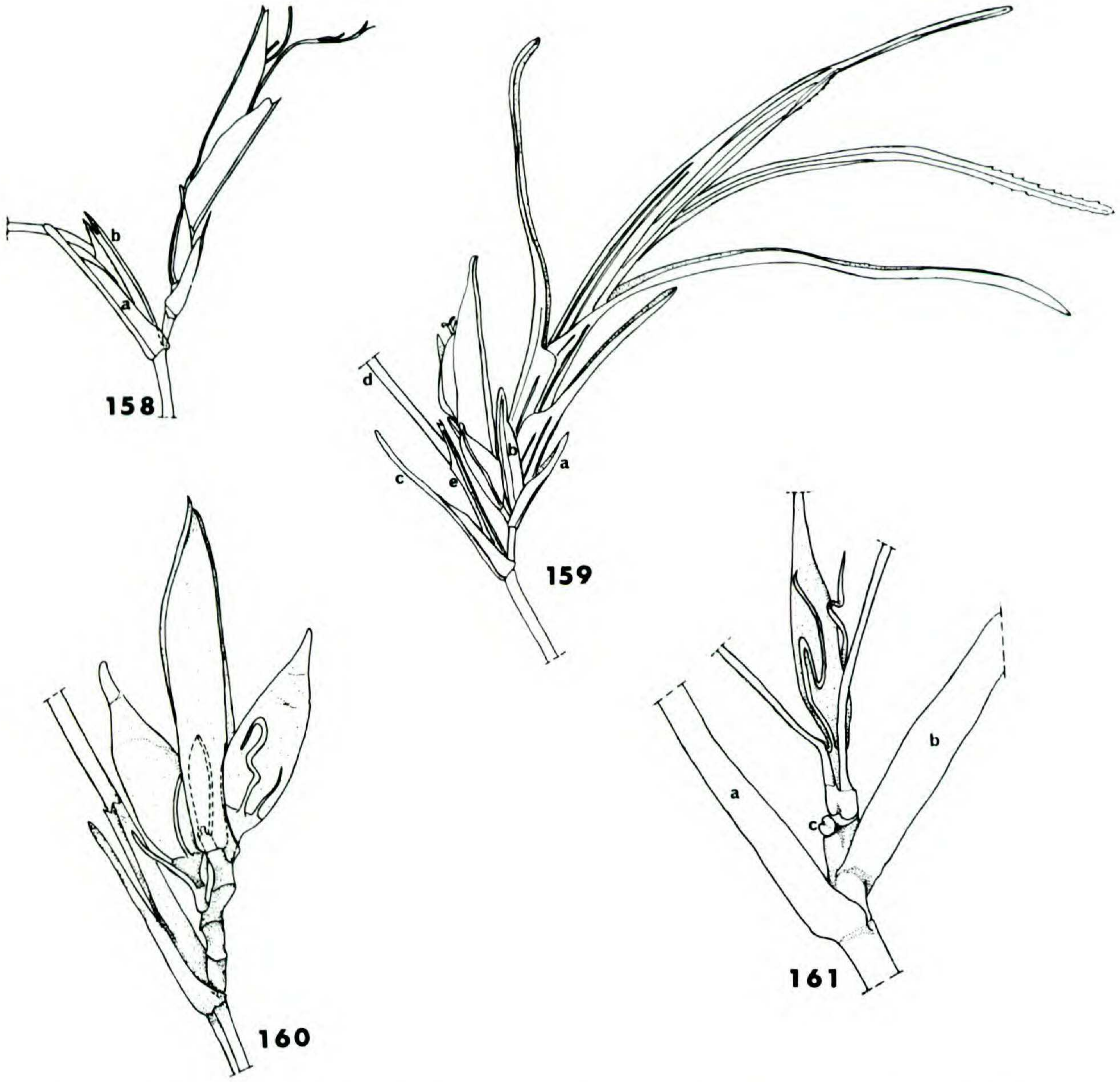
The lower rays emit subrays. At the node in which the basal long internode of a lower ray terminates, the second order axis turns aside, forming the basal internode of the subray. The upper rays do not emit subrays. Here the second-order axis terminates directly in a "lateral group." The last internode of a ray or subray ends in a "terminal group."

The expressions "lateral group" and "terminal group" are applied to the pseudospikelets and miniscule shoots which, together or alone, form the groups of organs that can be seen along the rays and subrays (Figs. 158–160). Among those examined, I found the lateral groups almost always composed of a single pseudospikelet (Figs. 158, 160), but sometimes it was composed of a pseudospikelet and an associated shoot (Fig. 159).

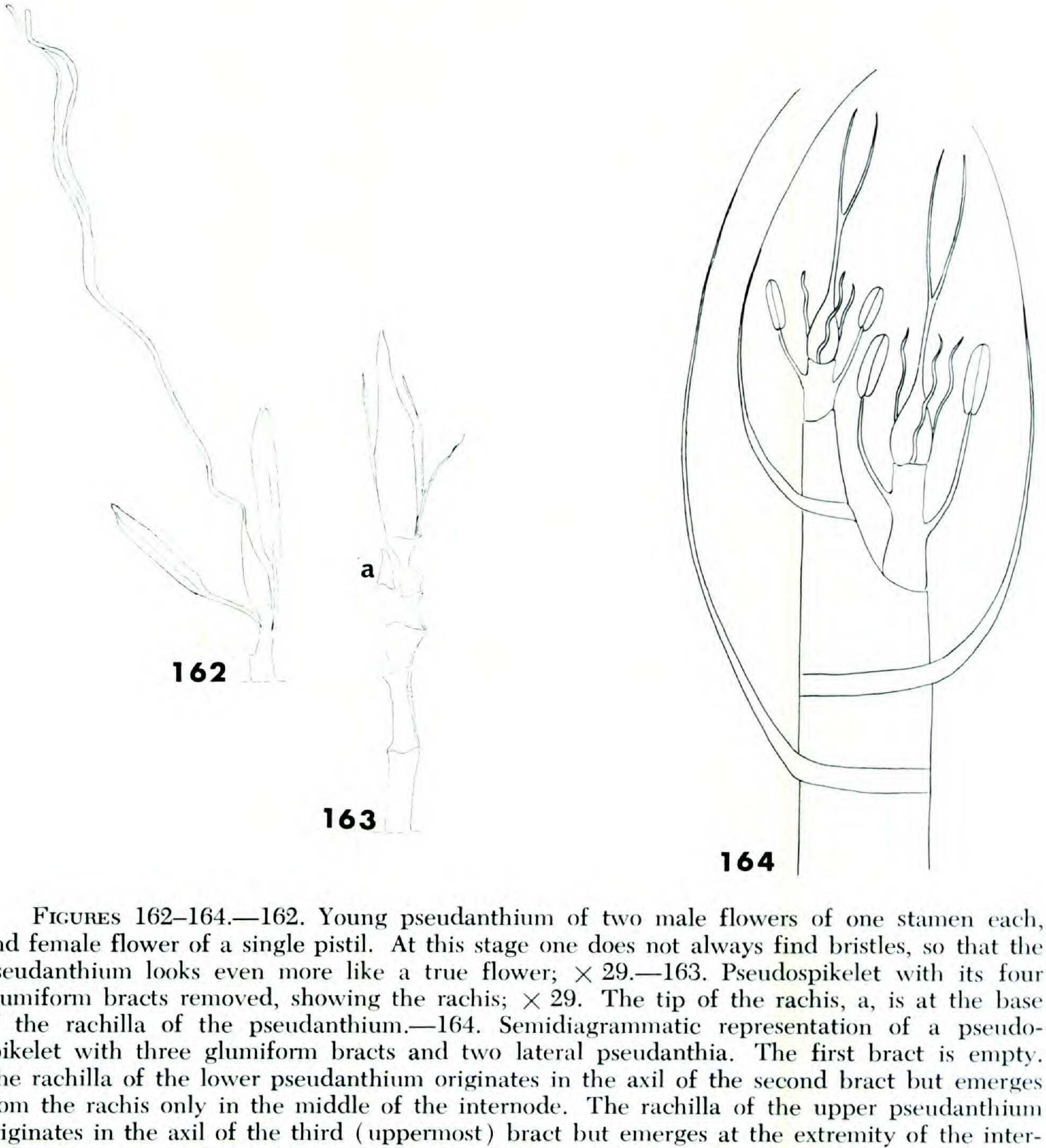
The terminal groups are usually composed of a pseudospikelet plus an associated shoot; very rarely the terminal group was made up of two shoots without a pseudospikelet.

In general, the second internode (first long internode) of an axis of branch order *n* forms the (*n*-1)th long internode of a ray or subray. The distal internodes of a branch form the axis of lateral or terminal groups. When a group is made up of a pseudospikelet and a shoot together, the axis of the shoot is a side branch that arises at the base of the pseudospikelet.

In one case examined a terminal group was made up of two shoots without a pseudospikelet. The axis of this group was of the fourth order; its continuation



FIGURES 158–161.—158. Part of a ray with a "lateral group"; × 8. The lateral group is here made up of a pseudospikelet (right) whose axis is the termination of the stem coming from below. Bract a, also on this stem, subtends a new branch whose first two basal internodes (a short one and a long one) continue the ray and which bears a prophyll, b, at the node which separates these two internodes.—159. Part of ray with a "lateral group"; × 8. This lateral group is made up of a pseudospikelet and a vegetative shoot. The stem from below continues on to form the axis of the pseudospikelet. Below the pseudospikelet is a bract, a, on the same axis. From its axil arises a new branch which forms the axis of the vegetative shoot. The first lateral organ on this new branch is a prophyll, b, which is part of the shoot. Further down the original stem is bract c, from whose axil arises a second new branch, d, which bears a prophyll, e, and which continues the ray.—160. Part of ray showing a "lateral group" formed of a pseudospikelet; × 14. The first, second, and third glumiform bracts have been removed, exposing the first four internodes of the axis of the pseudospikelet (rachis). The stipe of the fruit (rachilla of the true spikelet which forms the pseudanthium) to the left originates at the second node of the rachis but emerges in the middle of the third internode; the stipe of the fruit to the right originates at the third node but emerges near the top of the fourth internode. Both are cases of concaulescence. The fourth glumiform bract, shown at the top of the rachis, encloses a fifth bract (shown in dashed outline) which covers the tip of the rachis.—161. Pseudospikelet with basal glumiform bracts a and b spread apart, showing its one pseudanthium in fruit; × 33. The third glumiform bract was removed on the left side, leaving its scar and exposing a small bilobed projection, c, which is the apex of the rachis of the pseudospikelet. It appears lateral because of the development of the pseudanthium, which appears terminal. This pseudanthium really originates in the axil of the second bract, b, but remains concaulescent to



FIGURES 162–164.—162. Young pseudanthium of two male flowers of one stamen each, and female flower of a single pistil. At this stage one does not always find bristles, so that the pseudanthium looks even more like a true flower; × 29.—163. Pseudospikelet with its four glumiform bracts removed, showing the rachis; × 29. The tip of the rachis, a, is at the base of the rachilla of the pseudanthium.—164. Semidiagrammatic representation of a pseudospikelet with three glumiform bracts and two lateral pseudanthia. The first bract is empty. The rachilla of the lower pseudanthium originates in the axil of the second bract but emerges from the rachis only in the middle of the internode. The rachilla of the upper pseudanthium originates in the axil of the third (uppermost) bract but emerges at the extremity of the internode, appearing terminal. This rachilla appears to be a further extension of the pseudospikelet rachis, although it is really a new axis lateral to it. The base of the rachillas thus show concaulescence with the rachis.

formed the axis of the first shoot, and its only branch (a fifth-order axis) formed the axis of the second shoot.

Süssenguth described the pseudanthium ("Scheinblüte") as made up of a female terminal flower and a masculine flower of two stamens. Schultze-Motel (1959), in his discussion of *Micropapyrus*, repeats Süssenguth's description and

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the rachis internode and only emerges at the upper end of this internode near the rachis tip. The rachilla of the pseudanthium (with two filaments arising at different levels on it) appears to be a continuation of the pseudospikelet rachis but is really a new branch lateral to it. Two sinuous bristles arise at the base of the fruit.

illustration without disagreeing on the number of flowers in the pseudanthium or the number of stamens in the male flower. But, from the position of the stamens at different levels on the rachilla it is clear that each stamen is a separate male monandric flower. No undoubted pseudanthia are known in the Cyperaceae in which the male flowers have more than one stamen.

Süssenguth (1943) interpreted the hypogynous bristles as perianth or "intrastaminale Diskusorgane." Like Schultze-Motel (1959), I interpret the hypogynous bristles to be transformed bracts, that is, glumellas which have taken on the form of bristles.

I agree with Süssenguth that *Micropapyrus* is an independent genus. The structure of the inflorescence and type of pseudanthium justify its establishment. However, I disagree with his view that there is a relationship between *Micropapyrus* and the Rhynchosporeae. The latter have true spikelets and true flowers while *Micropapyrus* has pseudospikelets and pseudanthia. These structures are so different from those of the Mapanieae, however, as well as different from those of *Syntrinema*, that *Micropapyrus* should be placed in a new separate tribe, Micropapyreae.

Micropapyreae differ from the Mapanieae in the following characteristics:

1. The general habit of the plant and inflorescence are different.
2. The pseudospikelet consists of only 3–4(–5) large covering bracts with 1–2 pseudanthia instead of the dozens or hundreds of small covering bracts and pseudanthia of a pseudospikelet of the Mapanieae (expect for *Chrysithrix*).
3. The only glumellas present, the three at the base of the pistil, are in the form of bristles and not laminas as in all the Mapanieae.
4. The usual two lower, lateral, folded, ciliate-keeled glumellas of the Mapanieae are lacking.

Micropapyreae differ from the Syntrinemeae in the following characteristics:

1. The general habit of the plant and inflorescence are different.
2. The pseudospikelets are visibly separate bodies and not densely clustered in a head as in the Syntrinemeae.
3. The pseudospikelets are all bisexual instead of bisexual and male as in the Syntrinemeae.

Other differences between *Micropapyrus* and *Syntrinema* are more at the level of genus than of tribe, such as, in *Micropapyrus*, the presence of tiny vegetative shoots on the inflorescence branches, the lack of a subtending bristle with each male flower (stamen), the presence of two male flowers instead of three, and the sinuous, glabrous, hypogynous bristles rather than the straight, shortly hairy bristles of *Syntrinema*. In fact, the only similarity in the two genera is that both have relatively few pseudanthia per pseudospikelet and both have three hypogynous bristles in the bisexual pseudanthia.[3]

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[3] Since writing the above, I have seen two more collections of this species from Brazil, the first since the type; they were sent to me from Amazonia. These are: Pará, Rio Univini, Igarapé do Campo, 25 Apr. 1974, *Pires et al. 14257*. Pará, Rio Xerinini (Projeto RADAM, Ponto 07A, Quadrícula SA-20-X-A), *Pires et al. 13932*.

The plants of these two collections appear identical in habit to those of the type and have the same sympodial branching of the inflorescence rays. Like the type, the rays bear pseudo-

Micropapyreae L. T. Eiten, trib. nov. Pseudospiculae separatae dispersae secus ramos inflorescentiae; pseudospicula 3–4(–5) bracteis tegentibus et 1–2 pseudanthiis bisexualibus; quidque pseudanthium 2 floribus masculinis unistaminatis (sine glumellis subtentis) et 1 flore femineo unipistilato terminali (pseudoterminali?) cum 3 glumellis setiformibus hypogynis.

Type genus: *Micropapyrus* Süss., Bot. Jahrb. Syst. 73: 115–116. 1943.

WEBSTERIA SUBMERSA (C. Wright) Britton

(included in W. *confervoides* (Poiret) Hooper)

Description based on the following types: isotype fragment of *Scirpus submersus* C. Wright in Sauvalle, Fl. Cubana, 175–176. 1868: Cuba, *Wright 3775* (M); holotype and isotypes of *Websteria submersa* var. *negrensis* Süss., Bot. Jahrb. Syst. 73: 124–125. 1943: Brasil, Amazonas, Barra do Rio Negro, Oct.–Nov. 1819, *Martius 2810* (M); holotype and isotypes of *Websteria submersa* var. *leutzelburgii* Süss., Bot. Jahrb. Syst. 73: 125. 1943: Nordbrasilien [Território de Roraima], Paren-intôe, Serra do Sol, igarapé, in einem 3 m tiefen Wasserloch des Falls, Oct. 1927, *Luetzelburg s.n.* (M).

The plant grows submersed, carpeting lake bottoms, with roots fixed to the substrate and the culms buoyed up in the water or the upper part of the plant floating near the surface. It forms long thick stems from which whorls of culms arise at intervals (Figs. 166–168, 188–189). The culms are capillary, cylindric-sulcate or trigonous, slightly flattened and smooth. Many of the culms in a whorl branch at their tips forming new apical whorls; 4–19 culms per whorl were noted in the collections examined. The culms in the more distal whorls are progressively thinner, the last being 0.1–0.3 mm wide (Figs. 165, 170, 190). In some plants of other collections there are no long thick stems which give off whorls; instead a rooted whorl arises directly from the substrate, as a clump, and culms of this basal whorl have whorls at their tips, etc. (The "whorls" here referred to are shoots with the branching pattern shown in Fig. 110.)

The internodes between successive whorls are usually progressively shorter distally, except for the culms of the last whorl which may be very much longer than the internodes immediately below them (Figs. 165, 170, 190). Among the culms that make up a whorl, some form new whorls at their tips while others do not branch. The culms that have spikelets at their tips (peduncles) are longer, of equal length, or shorter than the other culms of the same whorl and are definitely thicker (Figs. 171, 190). The culms that arise from the whorl node (a compound node made up of a close succession of true nodes, one for each culm)

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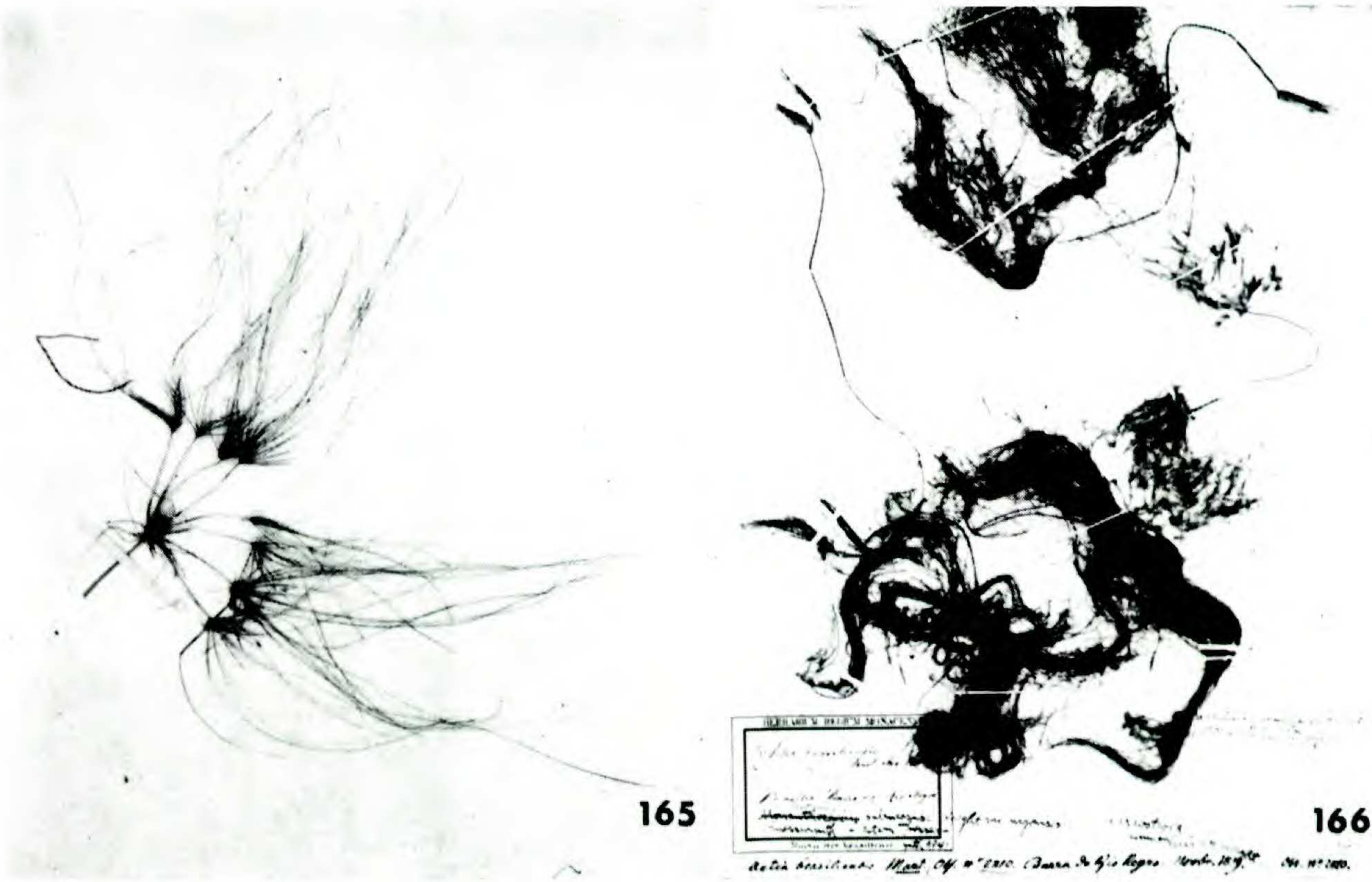
spikelets and miniscule shoots although in some of the inflorescences the latter are less frequent than in the type. The two new collections also have 1–2 pseudanthia in each pseudospikelet. The pseudospikelets are 3.0–3.5 mm long; the fruits are 1.5–1.8 mm long by 0.4–0.6 mm wide, with a dark honey-colored body and blackish brown apical point. The concaulescence of the stipe of the pseudanthium is such that it is embraced by the glume next above the one from whose axil it really arises. The hypogynous bristles are shorter, thinner, and straighter than those in the type collection. The level at which the stamens arise on the pseudanthium axis below the fruit is closer to the fruit base than in the type so that the conjunction of stamens and fruit make the pseudanthium appear even more like a true flower.

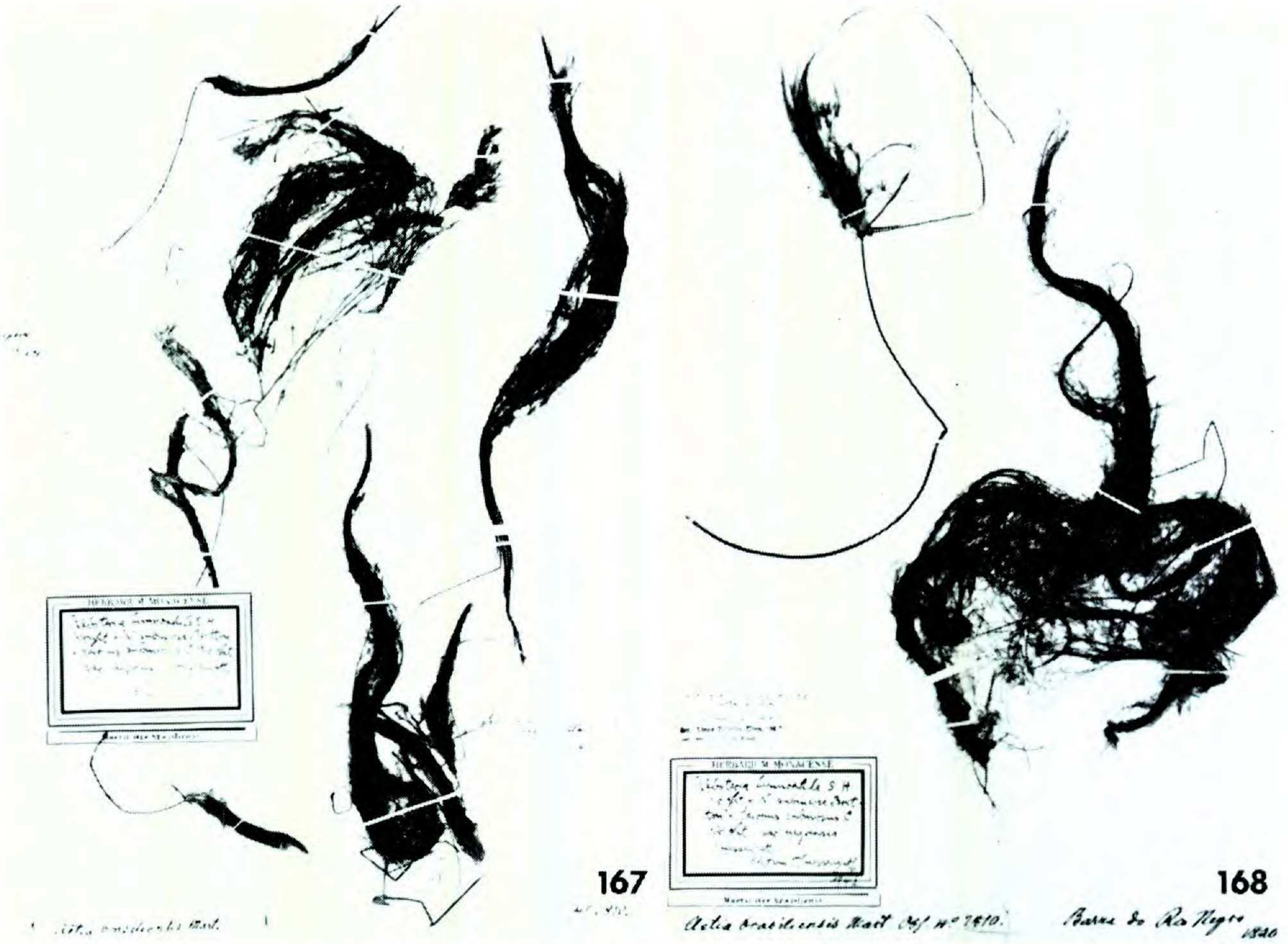


FIGURES 165–166.—165. Fragment of isotype of *Scirpus submersus* C. Wright, basionym of *Websteria submersa* (C. Wright) Britton; *C. Wright 3775*; × 0.2.—166. Lectotype of *Websteria submersa* var. *negrensis* Süss.; *Martius 2810*; × 0.2. Figures 170–187 were made from plants of this collection.

do not always develop simultaneously. Thus, in the same whorl with older culms may be found young culms still within their long, narrow hoodlike leaf sheaths.

Two scalelike bracts are found outside of and below each whorl (Figs. 169, 171, 191–193); the lower subtends the oldest culm in the whorl. It is triangular or elliptical, obscurely 3-nerved, 6.5–11.0 mm long and 0.6–1.6 mm wide in the lower whorls of a plant, and 0.75–2.0 mm long and 0.3–1.0 mm wide in the terminal whorls. This lower external bract has a median longitudinal thick portion streaked with reddish brown lines, an apiculate or blunt apex, and membranous sides whose margins in the material seen were partially or totally decayed. The upper external bract, although apparently "below" the whorl, is really distal to it on the culm whose tip bears the whorl. (This is also true in *Eleocharis* culm tip shoots; see Figs. 109 F, bract e; 110, bract b.) The upper bract is also triangular or elliptic with rounded apex; in the lower whorls it is 0.4–5.2 mm long and 1.6–2.0 mm wide, and in the terminal whorls it is 0.5–1.7 mm long and 0.2–0.8 mm wide. This bract does not have visible nerves; it is thinly membranous, hyaline and falls to pieces easily.

Within a whorl, between the culm bases, there are short or long triangular laminas with two convergent veins and an acute or obtuse apex (difficult to make out in Figs. 169 and 171; very visible in Fig. 191). These laminas are very thin and fall to pieces easily. It seems as if each lamina is associated with a culm, but due to ease of its decomposition in the water, there is almost never a correspondence between the number of laminas and culms. It is not possible to de-



FIGURES 167–168. Isolectotypes of *Websteria submersa* var. *negrensis* Süss.; *Martius 2810*; × 0.2. Figures 170–187 were made from plants of this collection.

cide from the plants themselves if these laminas are bracts subtending the culms or if they are prophylls and therefore on the same axis as the culms. They do not have the typical form of prophylls, that is, they have acute, not retuse apices; however, they do have the double venation characteristic of prophylls. Their exact position cannot be verified because the internodes between the culms making up a whorl are extremely short. However, since I believe *Websteria* evolved directly from *Eleocharis* and since in that genus the culm axes have basal prophylls, the similar laminas in *Websteria* are probably also of this organ.

The base of each culm is enclosed in two leaf sheaths (Figs. 169, 171, 191). The lower (outer) sheath is tubular, short, membranous, light-colored or tinged with reddish brown, and it has an oblique mouth; the upper (inner) sheath is long-tubular, membranous, light-colored or greenish, streaked with reddish brown lines, and it has an oblique mouth.

The apices of those culms that do not bear whorls or spikelets at their tips are bare and smooth; the tips are not covered by scalelike bracts as in *Eleocharis* (Fig. 203).

The peduncles bearing spikelets arise among the culms that form the antepenultimate and penultimate whorls. They are 2.3–5.1 cm long and 0.35–0.9 mm wide. They have two leaf sheaths; the lower decomposes easily. Sometimes it splits longitudinally on one side and so forms a lamina that may be confused with the basal lamina of the peduncle (prophyll), or it may become fragmented and

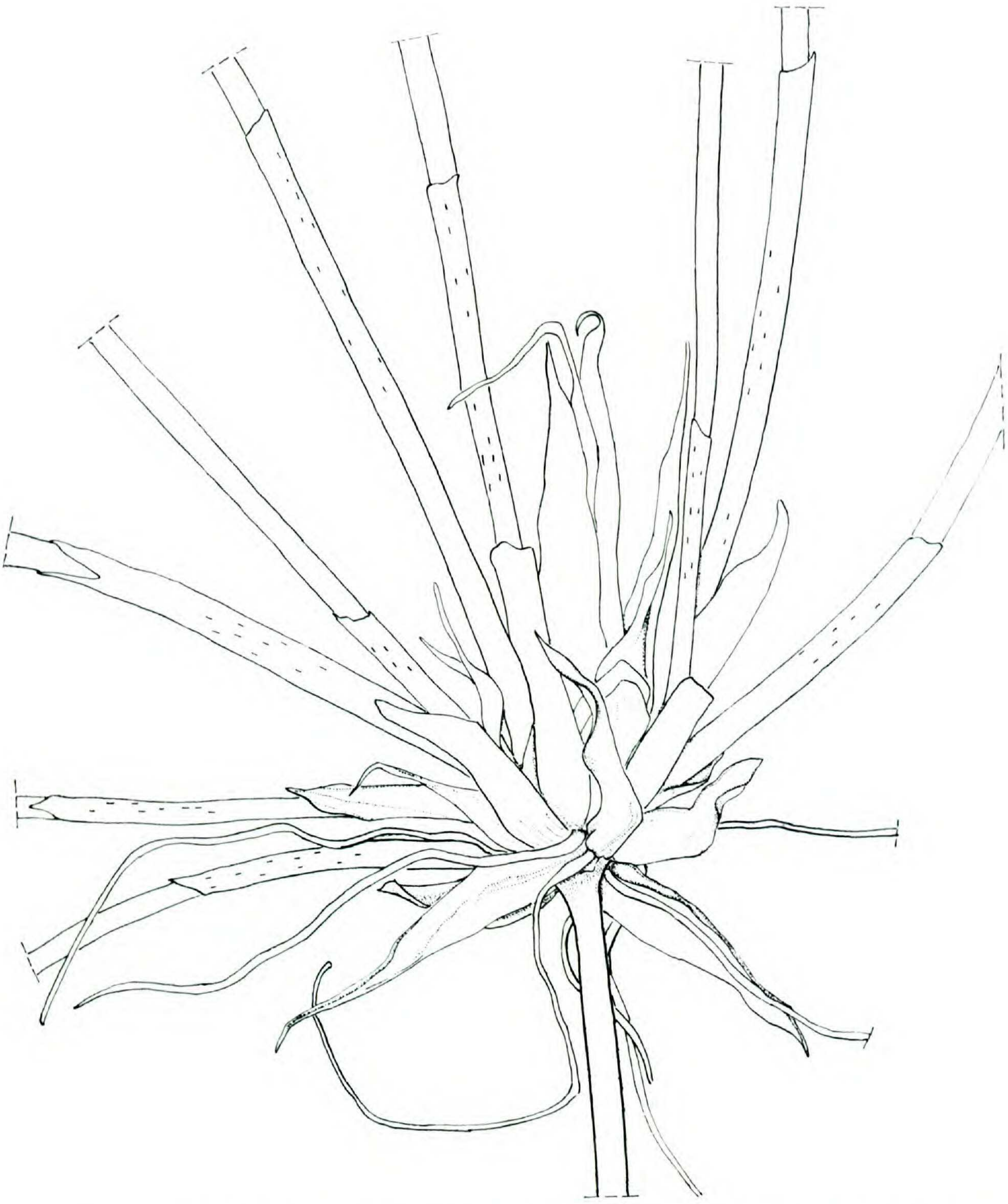
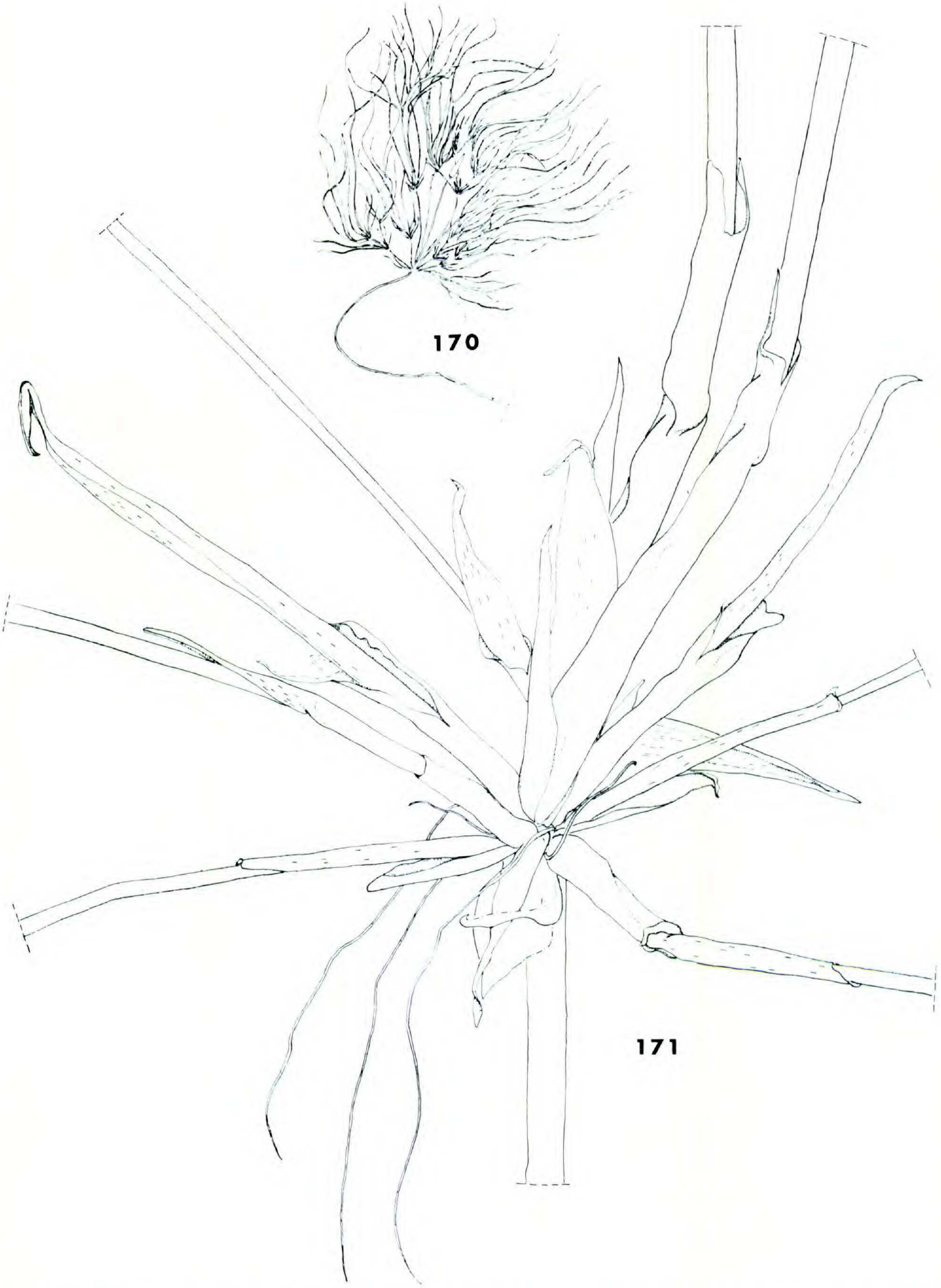
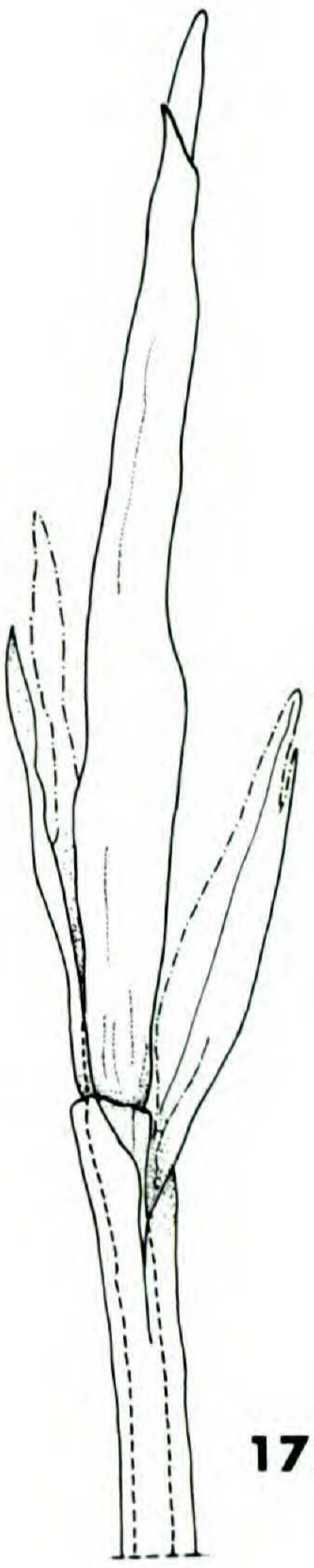


FIGURE 169. Detail of base of penultimate whorl; *C. Wright 3775*; × 16. Note from below to above, upper part of culm which bears the whorl, seven adventitious roots from culm bases, the two external bracts at the base of the whorl, base of nine developed culms with their two leaf sheaths (the upper streaked with short lines, the lower split open in some cases), and in the center several young culms still covered by their leaf sheaths. The prophylls were not seen and probably had rotted away.

disappear. The upper sheath covers the peduncle and its apex frequently covers the base of the spikelet (Figs. 172–173). This sheath is membranous and loose; its mouth is torn by the developing spikelet or decays or splits on one side, so that the apex of the sheath appears like a lanceolate leaf blade (Figs. 174–175).



FIGURES 170–171.—170. Branching of part of plant; × 0.4.—171. Detail of base of whorl; × 12. Note from below to above, tip of culm which bears the whorl, adventitious roots from culm bases, the two external bracts at the base of the whorl (one in front, the other behind the whorl at right), base of five developed culms and three young culms (the upper leaf sheath streaked with short lines, the lower sheath split open in some cases), and two thick peduncles with sheaths. The prophylls were not seen here and probably had rotted away.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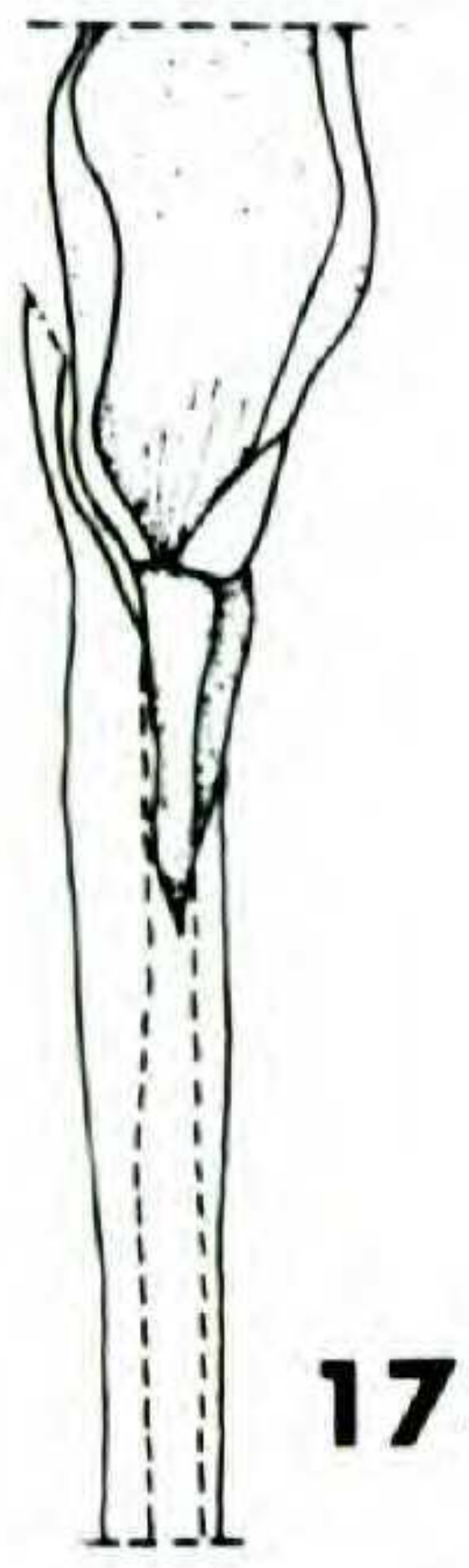
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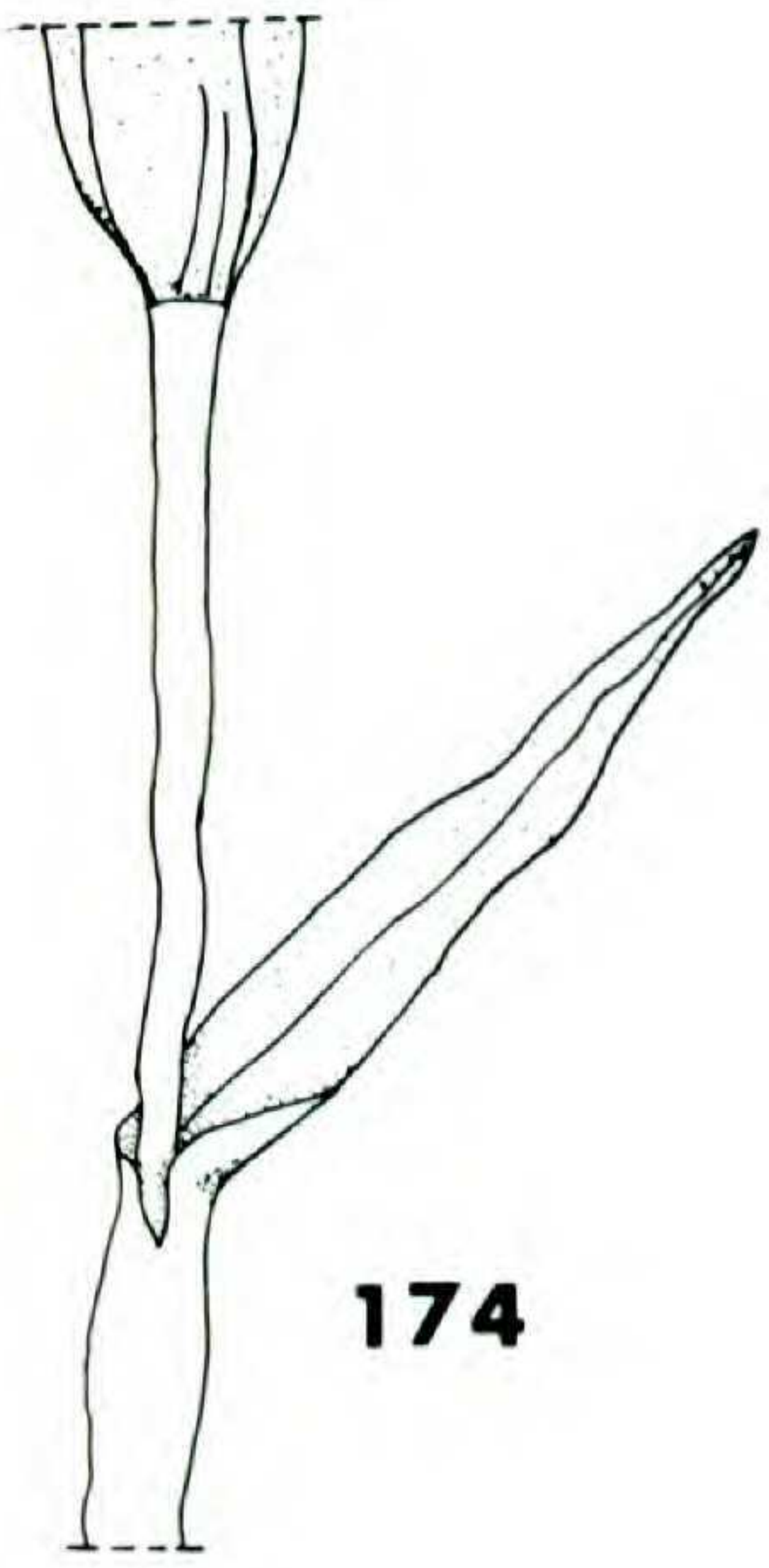
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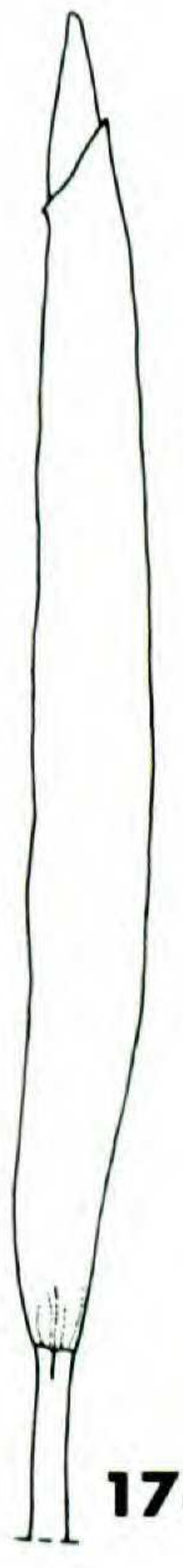
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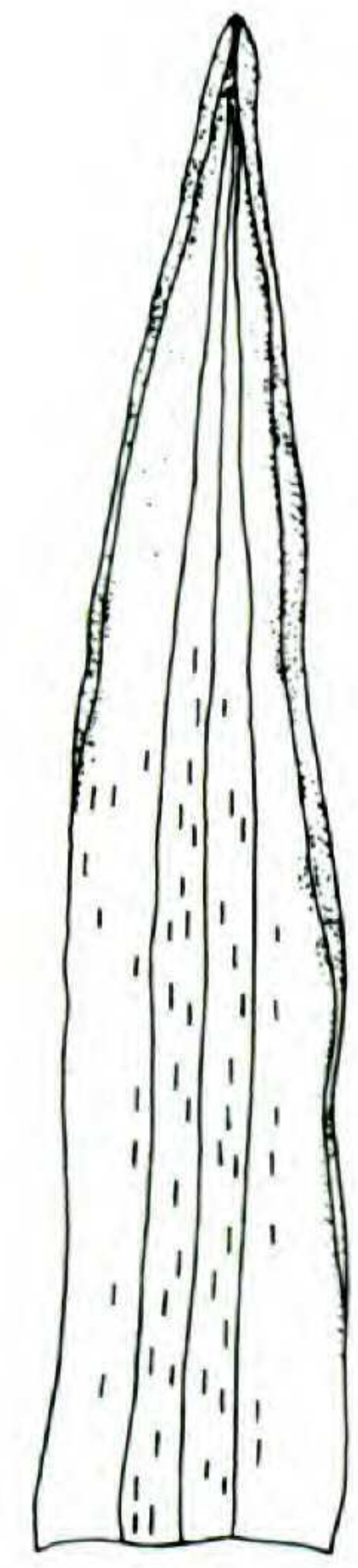
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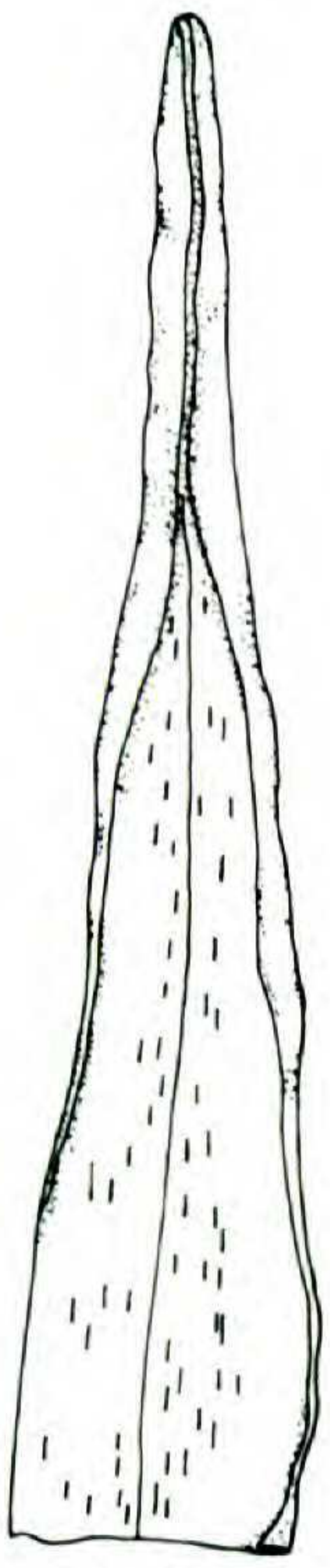
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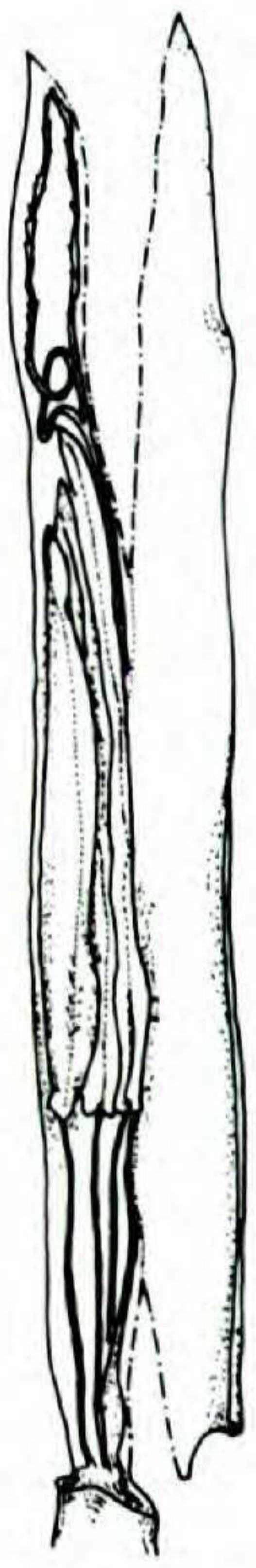
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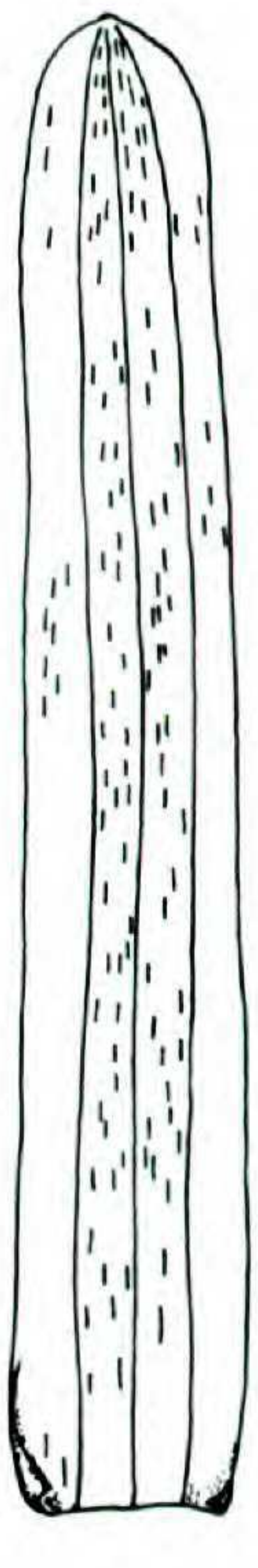
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Each peduncle bears one terminal spikelet (Figs. 176, 194, 199). The spikelets are long, elliptic or long-ovate, 9–11.7 mm long and 0.7–1.25 mm wide. Each spikelet always has a true glume (Figs. 178–179, 195) and a single flower; just below the spikelet and looking like it is part of an associated scale (Figs. 177, 180, 196, 198). The associated scale envelops the glume and has been counted in the dimensions of the spikelet as given above.

The associated scale is always empty. When still young, it forms a flattened tube with a vertical fold along the side opposite to its dorsal median portion (Fig. 183). The median portion is thicker and streaked with reddish brown lines. The inner true glume is membranous; when young, it is enrolled (Fig. 197) or it is tubular with a similar longitudinal fold which faces the dorsal part of the outer associated scale (Fig. 183). The true glume surrounds a bisexual flower. During development of the ovary, the tubular associated scale and glume split along the vertical folds whose tissue is initially thinner, and both laminas assume the typical form of glumes (Figs. 177–178, 184, 195–196).

The flower has three stamens with long-oblong anthers and a pistil with an ovoid-trigonous ovary and a long style with two long, pilose stigmatic branches (Figs. 179, 181, 200). Flowers may contain bristles (Figs. 181–182, 184, 200–201) or when young may still lack them (Figs. 179, 183).

The body of the achene is pyriform, 2.0–3.5 mm long and 1.5–2.1 mm wide. It has a subulate mucro 1.5–2.4 mm long with a vertical depression at its base reaching halfway up the mucro (Fig. 187). In other achenes (which perhaps are immature) the transition from body to mucro is wrinkled, at least when dry (Fig. 185). The surface of the achene is finely tuberculate with a hexagonal or pentagonal reticule (Fig. 186). There are 7–14 retrorsely spinulose bristles arranged in two series (Figs. 185, 187).

The material at present called *Websteria submersa* was originally described by Charles Wright (1868) as *Scirpus submersus*, based on *Wright 3775*, from lakes in Pinar del Río. It is sometimes still called by this name (Barros, 1960). Charles Wright described his plant as having 1-flowered spikes with two glumes; in anthesis the spikes were scarcely emersed and thereafter submersed. He considered the thick stems as stems and the thin stems as leaves. He mentioned 8–

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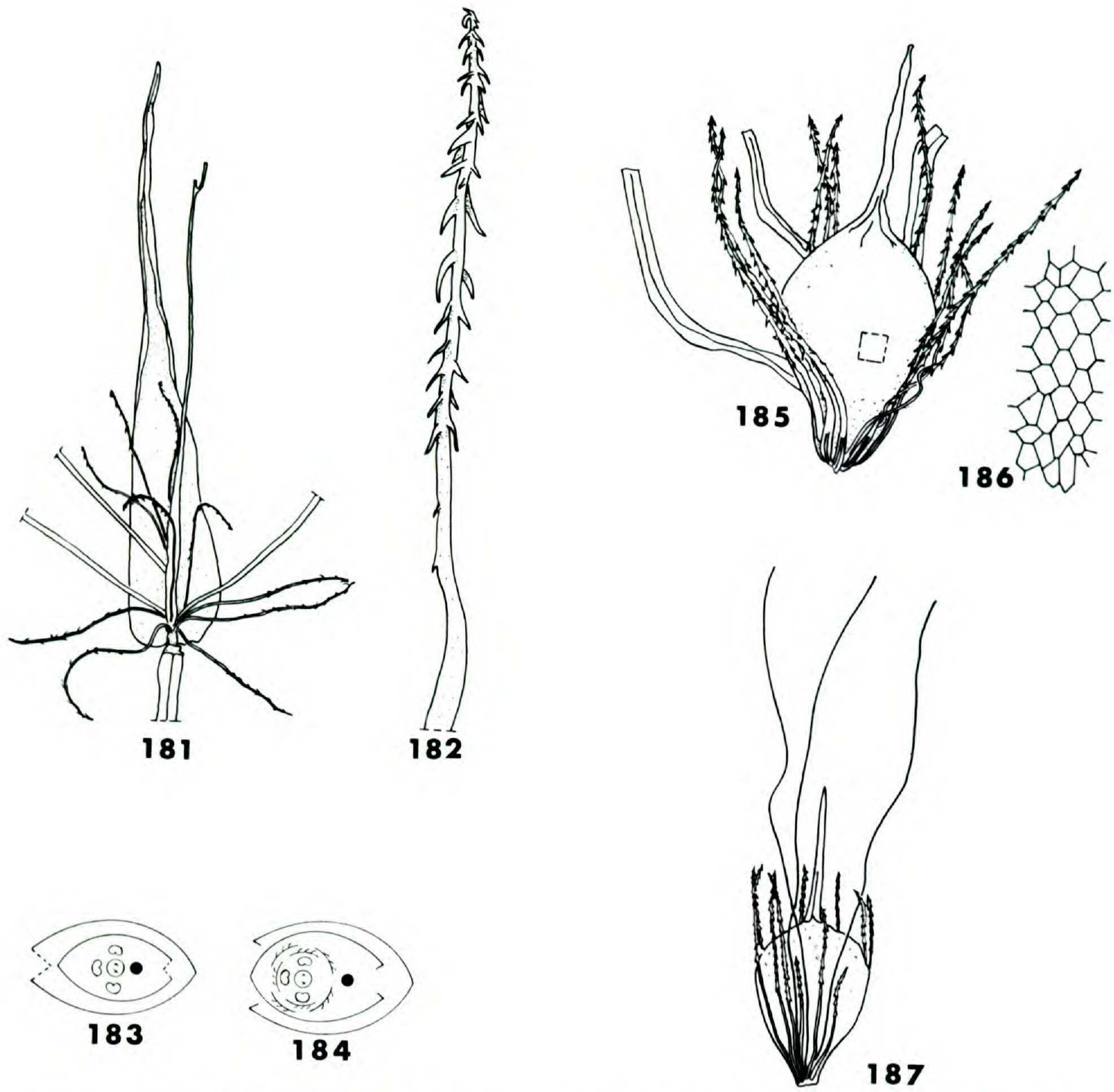
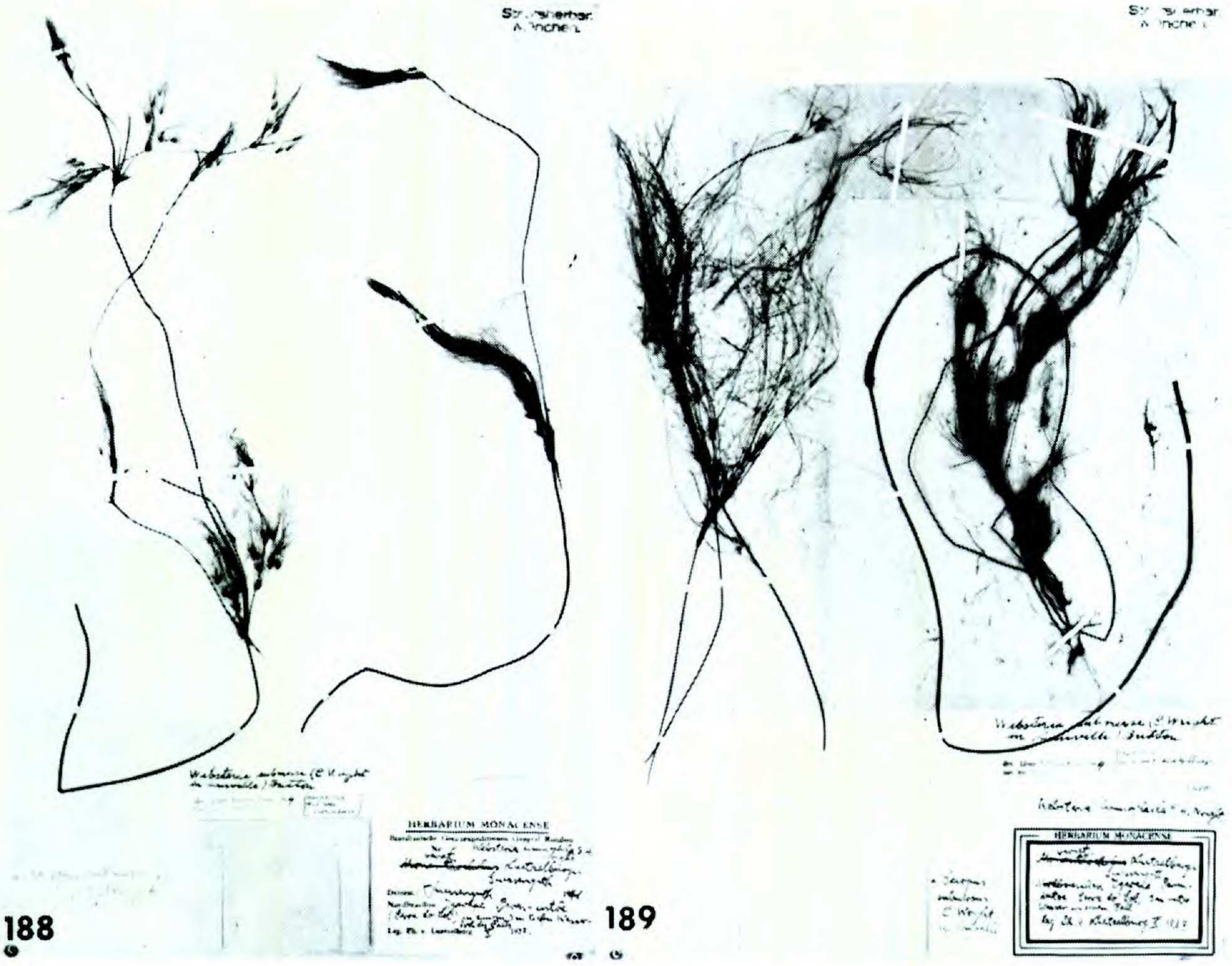
FIGURES 172–180.—172. Upper part of peduncle (in dashed outline) with spikelet; × 6.4. The upper part of the upper leaf sheath is here torn into three parts partially surrounding the spikelet.—173. Base of spikelet in fruit, showing separation of borders of associated scale and the very oblique mouth of upper leaf sheath; × 6.4.—174. Peduncle and base of spikelet; × 6.4. Mouth of upper leaf sheath has decayed on one side, leaving other side appearing like a leaf blade.—175. Diagram showing how this arises. Shaded area of apex of upper leaf sheath represents part which decays; the rest remains to form the pseudoblade.—176. Peduncle tip and spikelet with its enrolled associated scale and glume in natural position; × 6.4.—177. Associated scale spread out, showing adaxial side streaked with short lines; × 6.4.—178. Glume spread out, showing adaxial side; × 6.4. The upper margins are short-ciliate and are shown here slightly enrolled.—179. Spikelet with associated scale removed and glume cut open to show young flower; × 6.4. The pistil has a very small narrow ovary and two pilose stigmatic branches. There are three stamens. Note absence of bristles in this young-flower stage.—180. Associated scale spread out, showing adaxial face and three parallel veins convergent at apex; × 6.4.



Figures 181–187.—181. Spikelet in mature flower with associated scale removed and glume spread out; × 6.1. Note pistil with thin ovary, three filaments (only bases shown), and ten bristles.—182. Detail of a bristle showing retrorse hairs; × 25.—183. Floral diagram of a young spikelet with the associated scale and glume still closed, forming tubes. Dashed line shows fine tissue along which these tubes will later split. Note absence of bristles. The dark point represents the apex of the rachilla and its position is meant to show that the flower is really lateral (pseudoterminal).—184. Floral diagram of a mature spikelet with open associated scale and open glume and two series of bristles.—185. Mature achene with filament bases and bristles; × 9.2.—186. Detail of reticulated surface of achene in square area in Fig. 185; × 25. —187. Mature achene with bristles and filaments; × 6.2.

10 bristles for the achene. Samuel Hart Wright (1887) described a new genus, *Websteria*, with one species, *W. limnophila*, based on several collections: *S. H. Wright s.n.*, December 1886, and *G. W. Webster s.n.*, April–May 1886, both from lakes in Volusia County, Florida, U. S. A. Britton (1888) noted that the type of *Scirpus submersus* and those of *Websteria limnophila* belonged to the same species. Britton agreed with S. H. Wright that this species constituted an independent genus and therefore designated it *Websteria submersa* (C. Wright) Britton because *submersus* was the oldest epithet of those treated.



FIGURES 188–189.—188. Holotype sheet of *Websteria submersa* var. *luetzelburgii* Süss.; *Luetzelburg s.n.*, Oct. 1927; × 0.2. Figures 191–201 were made from plants of this collection. —189. Isotype sheet of *Websteria submersa* var. *luetzelburgii* Süss.; × 0.2.

After having seen the types of *Scirpus submersus, Websteria submersa* var. *negrensis, W. submersa* var. *luetzelburgii*, and one of the syntypes of *W. limnophila,* I concluded they all belonged to the same species. Because of its distinctive branching and habit and distinctive large 1-flowered spikelets, I agree that *Websteria* is an independent genus. It is neither a *Scirpus*, nor as Hooper (1973) reduced it, a species of *Eleocharis*.

I do not believe the two varieties erected by Süssenguth can be justified. The material of this species that was examined shows little variation between collections and such as there is can be expected in aquatic plants. No collection has characters so marked as to justify the erection of a variety. For this reason I have given a description based on the three types together.

It is now necessary to enter into a discussion of some Old World plants which apparently are part of the *Websteria* complex and to consider their relation to the New World plants. Poiret (1804: 755) published *Scirpus confervoides* from a specimen of Petit-Thouars from pools of water in Madagascar. Poiret thought the plant had a certain relation to *Scirpus fluitans* L. and apparently for this reason placed it in *Scirpus*. It had long stems with verticillate fascicles of elongated "leaves" finer than a hair. From the center of the fascicle arose 1–several filiform culms each with a basal sheath which was slightly lanceolate at its apex.

FIGURE 190. Isotype fragment of *Websteria submersa* var. *luetzelburgii* Süss.; × 0.85. It shows whorled, thin culms and thicker peduncles with spikelets.

Each culm terminated in a solitary oval "spike" composed of a few inner whitish membranous scales enveloped by two external subulate acute long scales. The description (there was no illustration) thus could be the same as *Websteria submersus* except for the extra inner glumes in the spikelet.

Various authors in the ensuing decades listed the name *Scirpus confervoides* but not all seemed to be referring to the same species. Kunth (1837: 173) described a specimen in the Willdenow herbarium, no. *1123* from Madagascar, under this name. (Willdenow had labelled it as *Schoenus confervoides.*) Kunth mentions crowded, fasciculate, long capillary "leaves" and large, linear, 1-flowered "spikes" with two glumes which are oblong, obtuse, trinerved, glabrous, the outer surrounding the inner. This could be a *Websteria.* Boeckeler (1869–1870: 487), on the other hand, says for his *S. confervoides*, "spiculis perminutis, ⅔ lin. circ. long.," which is certainly not a *Websteria.* He cites plants from Mauritius and South Africa but none from Madagascar. Clarke (1894: 653) later on also noticed this different sense for which Boeckeler used the name.

Miquel (1847: 225–226) described an *Eleocharis submersus*, which, according to him belongs to that part of the genus which Nees had earlier segregated as

Limnocharis. This use of the epithet "submersus" is previous to and independent of C. Wright's use of it under *Scirpus,* a fact which became confused later on when Durand & Schinz (1895) included Miquel's reference (under the incorrect generic name *Eleogiton*) in their synonymy of *Scirpus submersus,* and Clarke (1900–1901: 91) included it in his synonymy of *S. submersus.* As Süssenguth (1943) later on noted, Miquel's species is not a *Websteria* since the spikelet is described as 3–4 mm long, the lower glumes as "reliquae . . . multinerviae. . . ." and the habit like a flaccid form of *E. capitata.* The only collection cited by Miquel, from Surinam, is referred to as "Crescit ad plant. [ationem] Berlyn, l'Inquietude, sub aqua submersa, m. Sept." Walpers later on (1848–1849: 900) simply copied Miquel's description.

Miquel (1856: 303), in a flora of the East Indies, transferred *Scirpus confervoides* to *Eleocharis* (although with an interrogation) but ascribed the new combination to Kunth (1837: 173). However, Kunth had merely raised the possibility of the Willdenow plant being an *Eleocharis* by stating at the end of his description, "Eleocharidis species?"; Miquel was the first to actually list "confervoides" under *Eleocharis.* However, the collection he cites, *Jungh,* "Java, bij Batavia," may not be a *Websteria.* Miquel himself questions whether it is the same species as the Madagascar plant. Since he says his plant has "foliis longissimus," it is strange he considers it an *Eleocharis,* which does not have leaf blades.

Bentham (1881) published *Rhynchospora ruppioides* with an illustration. The text description was based on *Balansa 2550* from Paraguay and *Thwaites* from near Colombo, Ceylon. Bentham says he could find no difference between the two collections. By its branching, spikelet, flower, fruit and bristles, the plant illustrated is obviously a *Websteria.* Bentham did not relate his species to Poiret's *Scirpus confervoides* nor to the previously published *Scirpus submersus* of Charles Wright. He gave no explicit reason for including the plant in *Rhynchospora,* although it could have been, as Clarke later on (1900–1901) pointed out, because of its 1-fruited spikelet. Bentham described the plant as 1-flowered and with 3–4 glumes, but said these gradually increased [presumably in size] from the short outermost to the flower-bearing innermost ("Glumae 3–4, rigidae, ab extimo brevi ad intimum florentem gradatim auctae"), while Poiret had described the outer glumes as the longest. Also, Bentham twice stated that the species had 6 bristles per spikelet while his illustrations show 10. Therefore, it is possible he examined the spikelets of only the Ceylon specimen and included the Paraguay specimen in the same species from general similarity of habit, but the artist used the Paraguay specimen (which shows only two long glumes) for drawing the spikelets.[4]

In Charles Wright's (1868: 176) previous description of *Scirpus submersus* he mentioned Thwaites's Ceylon specimen which he apparently had seen. He said his own plant had the same habit but a different fruit and therefore was a new species. Since Wright referred to Thwaites's plant as "Sc. ruppioides Thw. e

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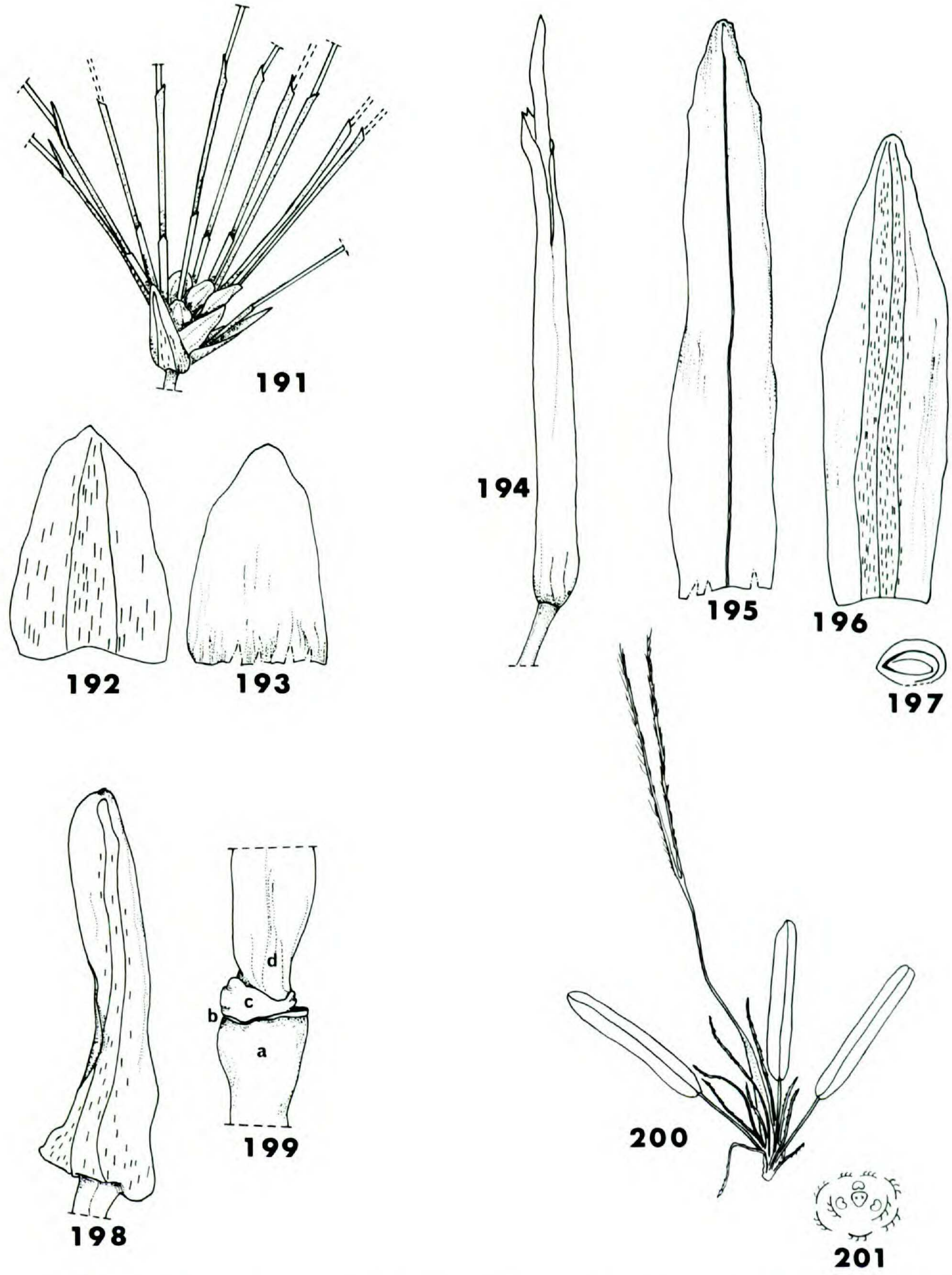
[4] In a letter to me Ms. Sheila S. Hooper states: "The habit drawing on the *Icones* plate is not an exact reproduction of the whole or part of either syntype—witness the curious thick 'branch' at the left side of the plate. But I think it is mostly taken from CP 3936 [the Thwaites specimen]. It could not have been wholly taken from Balansa 2550 which has no main stem to serve as original for the thick 'branch'."



FIGURES 191–201.—191. Base of a whorl; × 7. Note the two external bracts at base of whorl and the scales (prophylls?) among the culm bases with their two leaf sheaths. Culms shown in dashed lines had decomposed leaving only their empty leaf sheaths.—192. Lower external bract at whorl base; × 17. It is streaked with short dark lines and has a median thicker portion delimited by the two lines shown.—193. Upper external bract at whorl base; × 17. This is of thinner tissue than the lower bract and has no veins.—194. Spikelet with associated scale and glume in natural position; × 7. The associated scale is beginning to open by splitting. The glume inside it is convolute and projects beyond the associated scale.—195.

Ceylon," Thwaites had apparently given his plant a name on the label, a name whose epithet (under *Scirpus*) Bentham used (under *Rhynchospora*).[5] However, since Bentham did not indicate that he was taking the epithet from Thwaites, as well as his putting it under a different genus name, the author of *Rhynchospora ruppioides* is Bentham, as generally admitted, and not Thwaites ex Bentham.

Trimen (1885a: 103, 1885b: 140) cites Bentham's species in his species lists of Ceylon plants, mentioning specimen "C. P. 3936." This is Thwaites's specimen, the "C. P." standing for "Ceylon Plant" and the number being an accession number of the specimen in the Peradeniya Herbarium.

Clarke (1894) noticed the resemblance of the Ceylon plant and the Old World plants in general to Charles Wright's description of *Scirpus submersus*, and in fact used Wright's name for the Ceylon species instead of Poiret's earlier name without giving a reason. He states in synonymy, "S. confervoides *Poir. Encyc.* vi 755 (non Boeck.)," not, of course, because he thinks Poiret's name is a later homonym but because he thinks Boeckeler's use of the name is for another species; apparently he is referring to Boeckeler's 1869–1870 article which I have already mentioned. Clarke cited two Ceylon specimens for his *S. submersus*, *Thwaites* (C. P. 3936), and *Beckett*, and stated that the two lower [outer] glumes were concave and elliptic-oblong, the lower of the two empty and the next with a nut-bearing flower, while the upper glumes were smaller, sterile or bearing a male flower, or sometimes none. This description accords with Poiret's and is different from Bentham's text description.

Durand & Schinz (1895), in their conspectus of the flora of Africa, used the name *Scirpus submersus* and in their synonymy included Poiret's *S. confervoides* and the other names based on Old World plants as well as S. H. Wright's *Websteria limnophila*, but not Britton's new combination, *W. submersa*.

Lindman (1900: 21) lists *Balansa 2550* from Caaguazú, Paraguay, "dans les marais, april, 1876" (the collection Bentham had cited) under *Scirpus submersus* C. Wright. There is no description.

Clarke (1900–1901), under *Scirpus submersus*, gives in synonymy names from Old and New World plants and describes the spikelets as having more than two glumes ("glumis 2 imis 8 mm longis, glumis ceteris brevioribus, paucis masculis

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[5] This supposition was confirmed in Ms. Hooper's letter: "Thwaites had the plant from a Mr. W. Ferguson, who collected it in Colombo in February 1867 and he [Thwaites] wrote 'Scirpus ruppioides' and 'CP 3936' on it. Sketches for the Icones plate dissections are attached to one of the Kew sheets of it which ought to be the lectotype if two species are recognized." Of course, whether *ruppioides* is recognized as a distinct species from *confervoides* or not, the Thwaites specimen, CP 3936, should be chosen as the lectotype for the name *Rhynchospora ruppioides*. Although the drawings are attached to the Cyclon specimen, as stated the spikelet drawing may be from the Paraguay specimen because of the difference in bristle number.

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Glume spread out, with midvein; × 7.—196. Associated scale spread out, with three veins, the two lateral ones delimiting a thickened median portion; × 7.—197. Cross section of these laminas, in natural position in this spikelet.—198. Dorsal view of an associated scale; × 7.—199. Base of spikelet. a = tip of peduncle; b = scar where associated scale was attached; c = short internode between associated scale and glume; d = base of glume; × 28.—200. Flower; × 7. Filaments have not yet lengthened. Note bristles.—201. Floral diagram of this flower.

(?) aut rudimentariis vel 0"). The only collection he cites is the type, *C. Wright 3775*, but it is not clear if his description, especially as to the number of glumes, is based on original observation of this collection or if it is taken from his former description of the Ceylon plants. Like Poiret, Clarke thinks the species is close to *Scirpus fluitans* L.

Chodat & Hassler (1903: 1019–1020), in their flora of Paraguay, mention the species as *Scirpus submersus*, cite the collections *Balansa 2549, 2550*, and give *Rhynchospora ruppioides* and *Websteria limnophila* in synonymy. There is no description. The range given for the species is Madagascar, Ceylon, Java, Carolina, Cuba, Surinam, Amazonia Inferior and Paraguay, thus including plants which, as we have seen, are not all *Websteria*.

Chermezon (1937: 143), in his sedge flora of Madagascar, called the species *Scirpus confervoides*. He included *S. submersus* in synonymy but not S. H. Wright's nor Britton's *Websteria*. He cited three collections, that of Petit-Thouars (to whom he referred as Dupetit-Thouars), and two of Perrier de la Bâthie, and stated that the plant has flaccid translucent capillary "leaves" in bunches, the 2 lower glumes 7–10 mm long, the lower of the two sterile and the next fertile, and sometimes 1–2 very small thin upper glumes; generally there is only one fertile flower, rarely two. He gives the general distribution of the species as Gabon, Congo, Madagascar, Java, and tropical and subtropical America.

In Süssenguth's general discussion (1943), he gives the synonyms of both Old and New World plants, but apparently he thinks there are two species (he does not state so definitely) because he says: "Dagegen wird die typische Art von Bentham, Urban und Clarke . . . als eine Pflanze beschreiben, deren Ährchen mehr als 2 Spelzen besitzen," while C. Wright and S. H. Wright described their plants as having only the two long glumes. Since the material he examined from Brazil (and on which he based his two new varieties) has only two glumes in the spikelet, he considered them allied to the Cuba and Florida specimens and therefore used C. Wright's epithet "submersus" for this different species which he accepts as in the independent genus *Websteria*.

León (1946: 204) mentions *Websteria submersa* (Miquel) Britton (a combination never published) for the flora of Cuba but gives only the New World as its general distribution. He mistakenly gives Miquel as the original author of the epithet "submersus" instead of C. Wright. Probably he was thinking of Miquel's (1847: 225–226) *Eleocharis submersa*, which Clarke (1900–1901) cites, although Süssenguth (1943) had stated his belief that this refers to a non-*Websteria*-like species.

Barros (1960) in his sedge flora of Santa Catarina, Brazil, called the species *Scirpus submersus* and included *Rhynchospora ruppioides* and *Websteria limnophila* in synonymy. His illustration is obviously of a *Websteria*. He cites one collection from Santa Catarina and one from Rio Grande do Sul but states that the species also occurs in Paraguay and Missiones (Argentina) although it is not included in his previously published sedge flora of Argentina (Barros, 1947). He gives its general distribution as warm and temperate regions in both hemispheres. He mentions only two glumes for the spikelet.

Hooper (1972), without textual comment, transferred *Scirpus confervoides* to

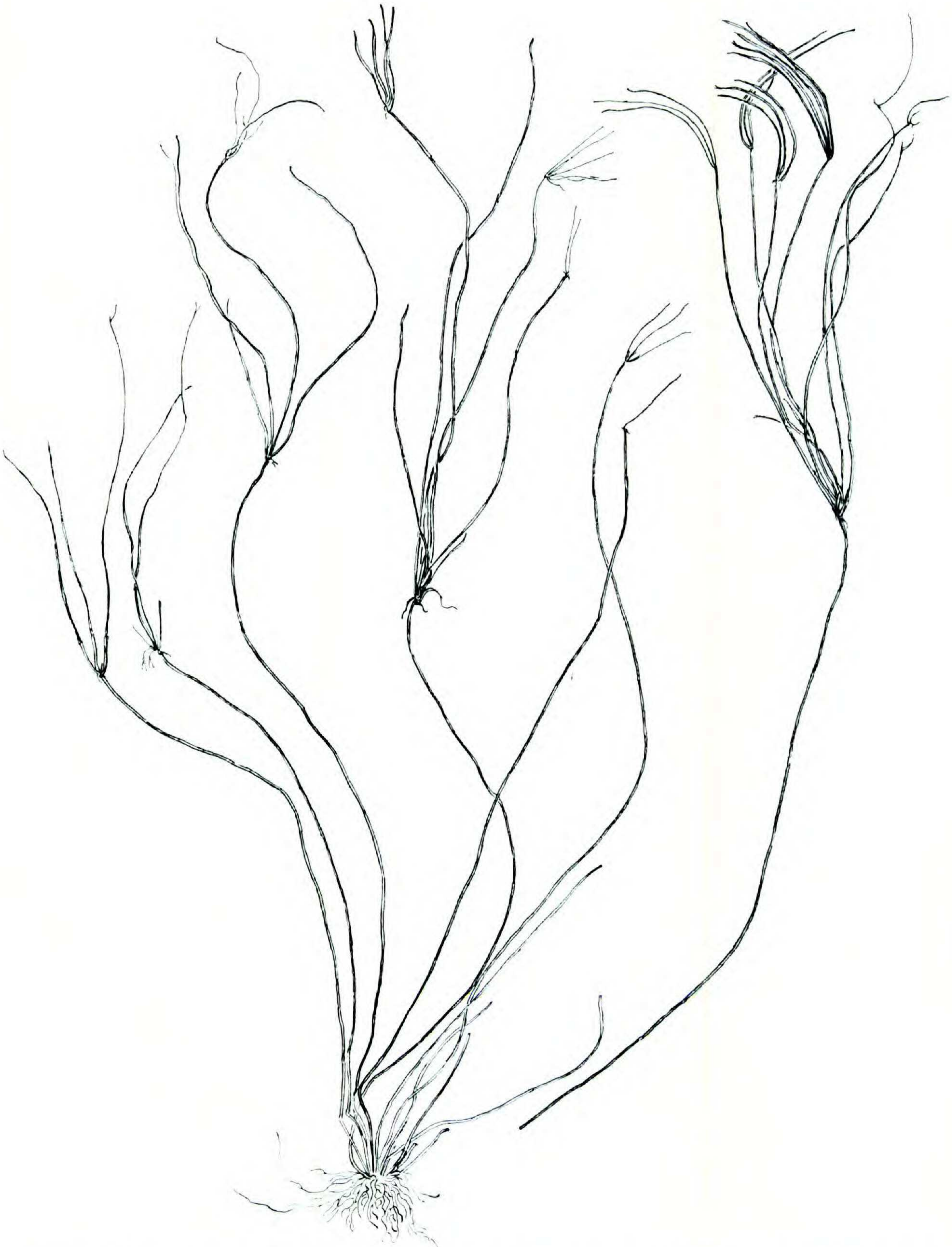

FIGURE 202. Habit of a sterile submersed plant of an undetermined species of *Eleocharis; Luetzelburg 12518*; × 0.5. The branching of this plant slightly resembles that of *Websteria.*

Websteria as a new combination and included only *Rhynchospora ruppioides* as a synonym. Since she did not include *Scirpus submersus, Websteria limnophila,* nor *W. submersa* in the synonymy, one could conclude that she considered the Old World plants to be a different species from the New World plants. However, in

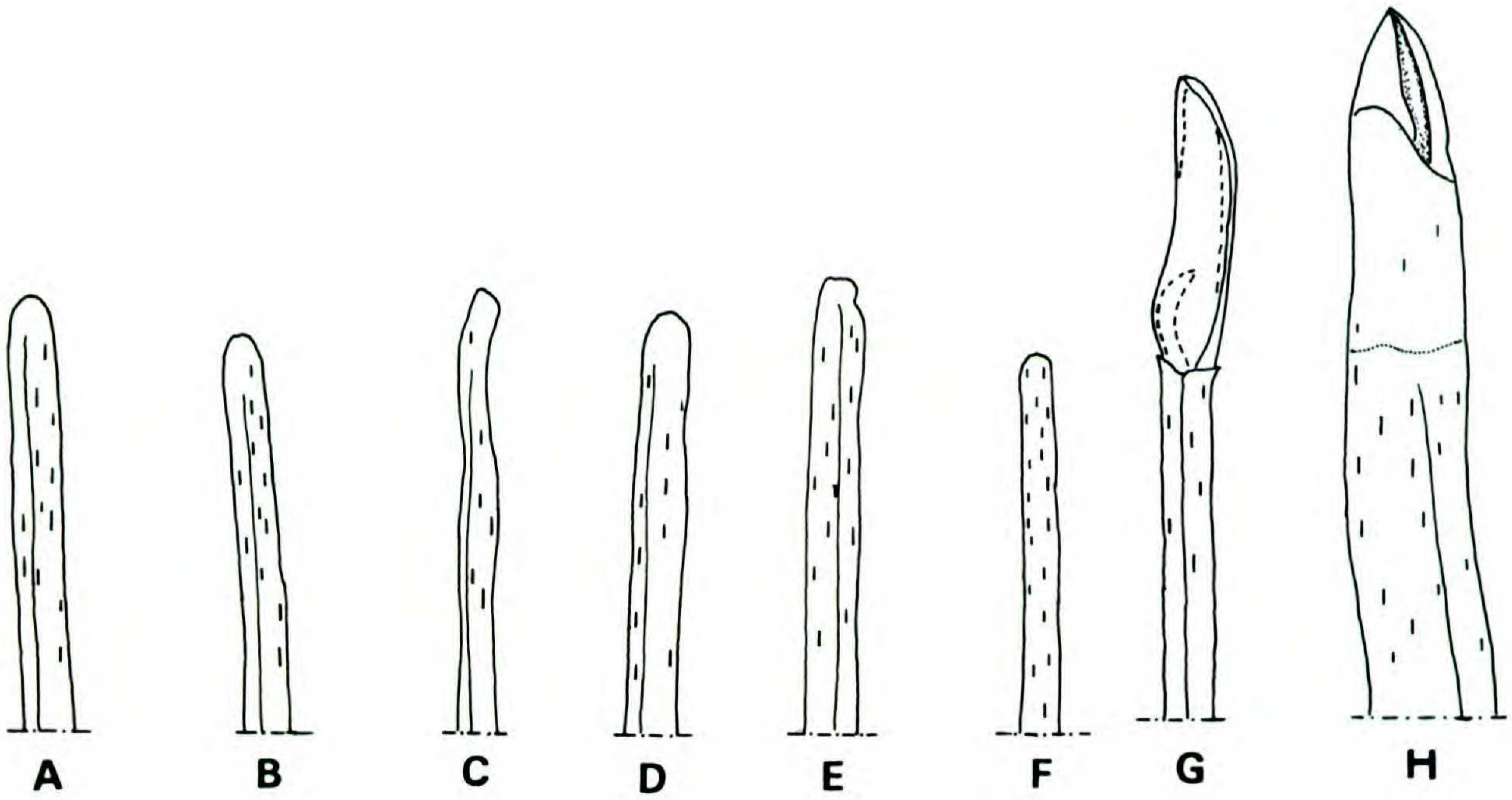

FIGURE 203. Culm tips of *Websteria*, A–F, and *Eleocharis*, G–H; × 40. In *Websteria* the culm apex lacks bracts; in *Eleocharis* spp. they are always covered by enrolled scalelike bracts.—A. *Pires et al. 3606*.—B. *Fróes 32156*.—C. *C. Wright 3775*.—D. *Luetzelburg 271*.—E. *Martius 2810*.—F. *Luetzelburg s.n.*, Oct. 1927.—G. *Luetzelburg 12518*.—H. *Luetzelburg 15051*. (Also see culm tips of *Eleocharis* species in Figs. 25, 65, 74–75.)

answer to an inquiry of mine about this, she stated that she thought they were all one species.

As mentioned, Hooper later on (1973), in a key to the genera of Cyperaceae for the world, sunk *Websteria* in *Eleocharis*. However, her letter to me stated that this was a previous opinion of hers which, since it was to appear in the third edition of Hutchinson's *Families of Flowering Plants*, was held up in its publication until this book was published. Her present opinion is that of her 1972 paper, that *Websteria* is a separate genus.

Thus, up to now, New World authors with the exception of Barros have not taken the Old World plants or the names based on them into consideration. Since Wright's publication of *Scirpus submersus*, the European authors (and Barros) have taken the New World plants and at least some of the names based on them into consideration but, with the exception of Süssenguth, have assumed that only one species was involved. Of these later authors, some put the species in *Scirpus* and some in *Websteria*, some used *confervoides* as the specific epithet and some, *submersus*, in the latter case without giving any reason why they used the later epithet.

I have examined one collection of *Websteria* from the Old World (Botswana, Northern District, Gobegha Lagoon, Okavango Swamp, 23°15′E 19°10′S, 1000 m, 5 March 1972, *Gibbs Russell & Biegel 1502*), and as far as I can make out, it is identical to the many I have seen from the New World. It has ripe fruits with bristles which look like the fruits of the New World plants illustrated in this paper. The fruit body color is a smooth shining ivory; the cells of the surface are not easily visible except those on the stylebase which have a slight tendency to be hexagonal. The ripe fruit examined was 3.5 mm tall, including the stylebase, and 1.7 mm wide, and had 11 bristles. The spikelets of this collection have only two large laminas (the associated scale and glume) and no smaller glumelike laminas outside or inside the large ones. These large laminas are a lightly purplish straw color, delicately streaked with purple lines. In one of the spikelets examined the associated scale was 8.7 mm long and the glume 11 mm long. The peduncles were unusually long, 7.8–9 cm, and 0.3 mm wide. The delicate sheath at the base of the peduncle was 21 mm long.

Since at least one Old World collection is plainly identical to the New World *Websteria*, it seems best to consider the whole genus as presently known to consist of one species. More Old World material would have to be examined to check on the reality of the presence of extra small "glumes" or more than one flower, but even if these really do occur but are not correlated with any other consistent morphological differences, they could be considered as vestiges of reduction such as are sometimes found in some but not all individuals of a species, without necessarily even calling for the creation of varieties. In any case there does not seem to be two distinct species. Bentham, as stated, also saw material from both the Old and New Worlds and considered them the same species.

As for the correct specific epithet, although I have not seen the type of *Scirpus confervoides*, we may provisionally use this epithet for the time being.

Websteria has always been described as having whorled filiform leaves (Poiret, 1804; C. Wright, 1868; S. H. Wright, 1887; Clarke, 1894, 1900–1901; Süssenguth, 1943). Actually, all of these "leaves" are filiform culms. The only organs of foliar tissue that *Websteria* possesses are the sheaths at the base of the culms and peduncles, the two basal external bracts of the whorls, the prophylls among the culms, the associated scale and the glume.

Some sterile collections from the Munich herbarium which I examined, *Luetzelburg 12518, 12528*, and *15051*, had been determined and were cited by Süssenguth as *Websteria submersa*. However, they are species of *Eleocharis* with a submerged-aquatic habit. The distinction between *Websteria* and *Eleocharis* is easily made considering the size of the associated scale and glume and usually the number of flowers in the spikelets. When the material is sterile, the two genera can be distinguished by the branching pattern (Eiten, 1964). But sometimes aquatic specimens of *Eleocharis* have a vegetative growth that approximates (but does not equal) that of *Websteria* (Fig. 202). However, the two genera can always be distinguished by examining those culm tips that do not bear whorls or spikelets. In all species of *Eleocharis* the culm apices are covered over by scalelike bracts (Eiten, 1969), while in *Websteria* there are no bracts visible; the apex is bare (Fig. 203).

Other collections examined (det. L. T. Eiten):

Websteria confervoides (Poiret) Hooper

UNITED STATES. FLORIDA: Volusia Co., lake SE of Lake Helen, Dec. 1886, *S. H. Wright s.n.* (US, syntype of *Websteria limnophila* S. H. Wright).

CUBA. *C. Wright 3775* (NY, US ex herb. Canby). PINAR DEL RIO: San Luiz, Laguna de Sancta Maria Chica, 20 May 1944, *Victorin & Alain* (NY).

TRINIDAD. Aripo Savanna, 8 Nov. 1961, *Richardson 2016* (NY).

GUYANA. Upper Mazarini River, 22 Sep.–6 Oct. 1922, *de la Cruz* (US).

BRAZIL. PARÁ: Mun. de Prainha, cabeceira do Rio Uruará, 3 June 1955, *Fróes 31936*

(IAN). Santa Izabel (40 km de Belém), 7 July 1968, *Pires 11879* (IAN). Lago do Macapichi, 1 Dec. 1955, *Fróes 32156* (IAN). Serra do Cachimbo, 425 m, 15 Dec. 1956, *Pires et al. 6306* (IAN). BAHIA: Rio das Contas, *Luetzelburg 271* (M).

I regard the sheet of *Luetzelburg s.n.*, Paren-intôe, Serra do Sol, Oct. 1927, (M), which had been marked as "Typus variet," as the holotype of var. *luetzelburgii*, the other sheet and the sheet with a fragment as isotypes.

All three sheets of *Martius 2810* were marked as var. *negrensis* by Süssenguth without stating which he considered the holotype. The first specimen has written on the bottom of the sheet: "Aetia brasiliensis Mart. Obs. n° 2810. Barra do Rio Negro. Novbr. 1819. Obs. n° 2810." The second sheet says: "Aëtia brasiliensis Mart. n° 2810." The third says: "Aetia brasiliensis Mart. Obs. n° 2810. Barra do Rio Negro 1820." I hereby chose the first sheet as lectotype. The others become isolectotypes. Martius's name, "Aëtia brasiliensis," was never published, which is a pity for he was the first to recognize this genus as independent.

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